# Marine trophic cascades

## Synergistic effects of fishing and eutrophication

university of groningen

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# Marine trophic cascades:

## Synergistic effects of fishing and eutrophication

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door

Katrin Reiss

geboren op 12 augustus 1979
te Frankfurt an der Oder, Duitsland

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# 1

# General Introduction

Katrin Reiss

# 1

"Between one-third and one-half of the land surface has been transformed by human action; the carbon dioxide concentration in the atmosphere has increased by nearly 30% since the beginning of the Industrial Revolution; more atmospheric nitrogen is fixed by humanity than by all natural terrestrial sources combined; more than half of all accessible surface fresh water is put to use by humanity; and about one-quarter of the bird species on Earth have been driven to extinction.

[...]

We live on a human-dominated planet."

Vitousek et al. 1997

1

Human history has driven rapid degradation of ecosystems all over the world (Lotze et al. 2006), especially since the development of agriculture and livestock farming 7,000 to 5,000 years BC. From 1,000 AD to the 20th century, rapid human population growth, increasing demands on the environment, commercialisation of resource use, the development of luxury markets, industrialisation and technological progress have led to phases of rapid resource depletion and the degradation of ecosystems (Lotze et al. 2006). Coastal zones are one of the most productive environments providing a wide range of ecosystem services including nutrient cycling and food production (Martínez et al. 2007) and 41% of the global population presently lives within the coastal zone. The calculation of an economic value of ecosystem goods and services showed that coastal ecosystems contribute 77% to the global ecosystem services value (Costanza et al. 1997). Besides the economical value, the coasts have a high ecological and social importance. Coastal ecosystems are subjected to multiple anthropogenic impacts, however, and the continued use of coastal ecosystems for living, recreation, food production and more necessitates the need for a sustainable management of the coastal resources.

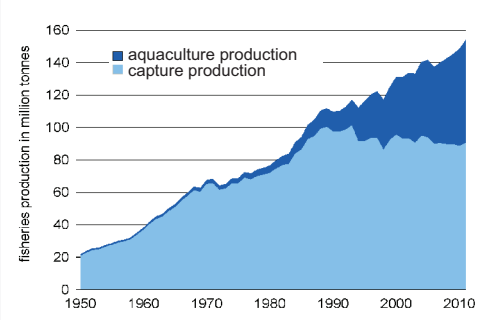
In this thesis, I examine the joint effects of two anthropogenic stressors on marine ecosystems: fishing (Box 1.1) and nutrient pollution (Box 1.2). Fishing is a much older pressure on marine ecosystems than the excessive input of nutrients. Marine fisheries were well established in Mesopotamian and Mediterranean trade about 3,500 years BC (Caddy and Cochrane 2001). Accordingly, overfishing or the unsustainable depletion of fish stocks was among the first of many human disturbances on coastal ecosystems beginning in the 16th to 19th century (Jackson et al. 2001). Since 2009, 30% of the wild marine resources have been overexploited or depleted and 50% are at their limit of exploitation (FAO 2012). In contrast, an excessive input of nutrients, which can lead to an increase in the supply rate of organic matter or eutrophication, is of more recent concern. Problems caused by eutrophication first gained broad scientific and public awareness in the 1970s and in 1990, coastal eutrophication was recognized as one of the major causes of immediate concern in the marine environment (Nixon 1995).

Fishing and eutrophication may interact and have unexpected synergistic effects on the environment. The removal of top-predators may eventually decrease grazing pressure, and overfishing may therefore be a precondition for eutrophication effects such as high loads of ephemeral algae (Jackson 2001). Eutrophication may lead to hypoxia and harmful algal blooms, both of which can cause fish kills (Vitousek et al. 1997); furthermore a shift in algae composition towards fast-growing algae could affect the species composition of entire food webs through bottom-up effects.

The Baltic Sea is a brackish water sea that has been subjected to both a strong fishing pressure and highly elevated nutrient loads, which have induced both changes in fish communities (e.g. Hansson and Rudstam 1990, Österblom et al. 2007, Eriksson et al. 2011) and large scale eutrophication (e.g. Cederwall and Elmgren 1990, Jansson and Dahlberg 1999, Gustafsson et al. 2012). The brackish environment and the resulting low biodiversity of the Baltic Sea may increase its vulnerability to external stressors (Chapin et al. 2000, Sokołowski et al. 2012) (see pages 30-31). At the same time, low species diversity simplifies the food web, which makes the Baltic Sea well suited as a study system for food web analyses.

The general aim of this thesis is to investigate the interrelationship between the removal of top-predators and elevated nutrient loads on the coastal Baltic Sea food web. A particular focus is on the functional composition of the herbivore community as a key trophic link for transferring both top-down and bottom-up effects. As a study system, I use a food web consisting of top- and meso-predatory fish, invertebrate herbivores and fast growing macro- and microalgae (see page 47). Using experimental approaches, I describe joint effects of fish composition and nutrient enrichment on herbivore and algal assemblages. In Chapter 2, I manipulated the presence of larger predatory fish and nutrients in a small-scale field experiment. In Chapter 3, I focus on the consequences of changing fish community composition in a field experiment. In Chapter 4, we manipulated the herbivore composition in a mesocosm experiment. In Chapter 5, I manipulated the fish composition and nutrient availability in a large-scale field experiment. Finally, in Chapter 6, long-term monitoring data of functional groups of fish are used to analyse food web effects across ecosystems. Finally, a summary of the main findings is given in Chapter 7.

## Box 1.1 Facts about fishing




modified after FAO 2012

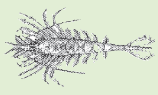
**World capture fisheries and aquaculture production**

- In 2011, capture fisheries and aquaculture produced 154 million tonnes of fish.
- Aquaculture production has increased by almost 12 times from 1980 to 2010.
- Food fish supply per capita increased from an average of 9.9 kg in 1960 to 18.8 kg in 2011.
- 50% of the landings are composed of only 20 species.

FAO 2012

captured or cultivated organism groups are:

vertebrates



invertebrates

algae

**consequences of capture fisheries**

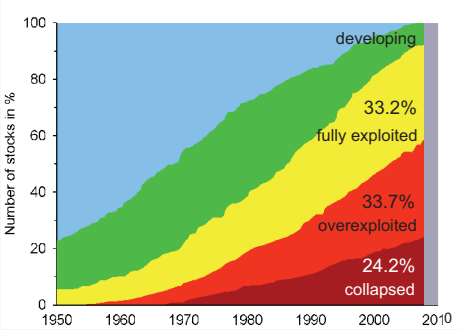
- decreasing mean size and age of fish
- changes in sex ratios and reproductive output
- changing growth rate
- changes in species composition and diversity of fish and benthos
- habitat destruction
- bycatch and discard

Jennings et al. 2001

**consequences of aquaculture**

- high organic and nutrient loads
- release of chemicals (therapeutants, antifoulants)
- introduction of pathogens
- introduction of new genetic strains
- habitat destruction (e.g. clearing of mangroves)

Wu 1995




modified after Froese et al. 2012

**Trends of global FAO catch data**

- developing stocks: catches are below the maximum production
- fully exploited stocks: catches are very close to their maximum sustainable production
- overexploited stocks: produce less than 50% of their previous maximum
- collapsed stocks: produce less than 10% of their previous maximum
- rebuilding stocks (not shown): recover from collapsed to fully exploited status, 1% with no increase

Froese et al. 2012

## Box 1.2 Facts about eutrophication

**causes**

- input of inorganic nutrients
- decrease in water turbidity
- change in hydraulic residence time of water
- decline in grazing pressure

Nixon 1995

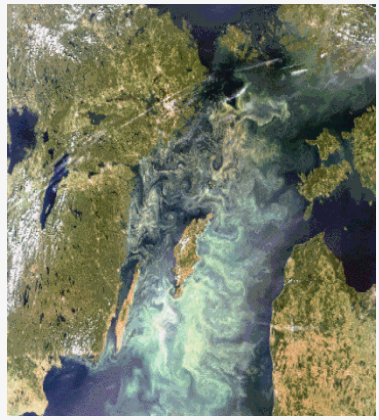
**eutrophication:**

increase in the supply rate of organic matter

**consequences**

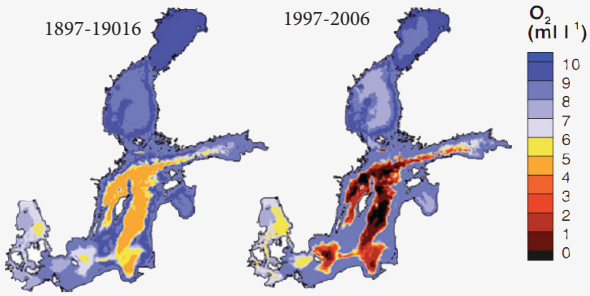
- shift from slow-growing seagrasses and large macroalgae to fast-growing macroalgae
- ultimate dominance of phytoplankton
- increased (harmful) algal blooms and gelatinous zooplankton
- decrease in water transparency
- oxygen depletion
- increased incidence of fish kills
- reductions in harvestable fish and shellfish biomass
- taste, odour and drinking water treatments problems
- decreases in perceived aesthetic value of the coast and water body

Duarte 1995, Smith and Schindler 2009



Extensive algal bloom in the Baltic Sea in 2005 www.smhi.se

High production of microalgae in the Mönsterås study area in summer 2008




from Gustafsson et al. 2012, with permission from the copyright holder (Royal Swedish Academy of Sciences)

**The average bottom water oxygen concentration**

has decreased dramatically during the last century and forms extensive anoxic zones.

Recent simulations indicate that no improvement in water quality of the Baltic Sea can be expected, but decrease in nutrient loads only maintain the status quo.

Gustafsson et al. 2012

## 1. Food Webs

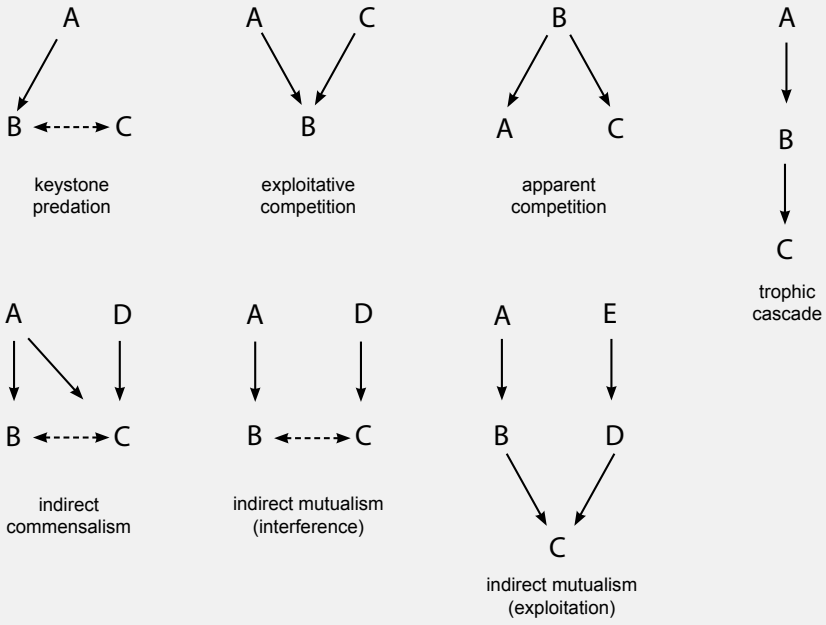
The activity of any organism affects not only other organisms but also its environment (and *vice versa*) (Begon et al. 2006). Therefore, ecological interactions are always part of complex ecological networks. Interactions between species embrace many different phenomena from the competition for space between barnacle species in the intertidal to the symbiosis between ruminants and the microorganisms in their stomachs. There are many types of ecological interactions: consumer-resource interactions, interactions between organisms and the environment, spatial interactions, non-trophic direct interactions (e.g. behavioural interactions), chemical and physical interactions that together build ecological networks (Olff et al. 2009). All these networks will always operate simultaneously (Olff et al. 2009) and their mutual interplay may explain why a community or an ecosystem is more than the sum of its parts.

The network, which connects consumer-resource interactions, is the food web. In consumer-resource interactions, predation is one important interaction mode, but the consumption of resources does not always mean predation. For instance, detrivory or nectar feeding are consumer-resource interactions, but have no predator and prey. Thus, predation is the consumption of one organism (prey) by another (predator), in which the prey is alive when the predator first attacks it (Begon et al. 2006). There are two main classifications for predators. One discriminates carnivores (consuming animals), herbivores (consuming plants) and omnivores (consuming both), the other distinguishes true predators (take all of an individual prey, which dies more or less immediately after the attack), from grazers (remove only parts of many prey individuals, which rarely die on the short-term), parasites (in contrast to grazers attack only few individuals during their life) and parasitoids (associated with a single host individual, no immediate harm but eventually lethal). By this definition, grazers may also consume parts of animal prey as long as they are not killed immediately, e.g. dab feeding on brittle star arms (Duinelveld and van Noort 1986). Predation constitutes direct links between trophic levels in food webs and often predators have large effects on the density and distribution of their prey. In this thesis I examine the importance of predation in a food web context by testing the consequences of a predator decline and changes in predator composition for the structure of the food web. Therefore, predation will form the key element in this thesis, but also non-trophic interactions will be discussed.

## Trophic Cascades

Direct effects in predator-prey interactions imply the direct consumption of one species by another species. As a direct effect of a decrease in predator density, we expect a higher density of its prey. However, predator-prey interactions can also have indirect effects on non-prey species. Wootton (1994) described indirect effects to occur "when the impact of one species on another requires the presence of a third species." For example, one species can indirectly affect a third species through the consumption of a common resource species (exploitative competition, Box 1.3). Six different types of indirect effects are commonly described in nature: *i)* keystone predation, *ii)* exploitative competition, *iii)* apparent competition, *iv)* trophic cascade, *v)* indirect commensalism and *vi)* indirect mutualism (Box 1.3). Of these, trophic cascades have probably received the most widespread attention in the scientific literature (see pages 17-18). Trophic cascades are by definition inverse changes between the relative densities of predator and prey in an at least three-level food chain with often striking effects on primary producers (Pace et al. 1999). Thus, in a three-trophic-level food chain, a trophic cascade means that increasing densities of third-trophic-level carnivores lead to direct negative effects on second-trophic-level herbivores, which in turn lead to indirect positive effects on first-trophic-level plants or algae (Box 1.4). Global declines in large predatory species have restructured ecosystems through trophic cascades all over the world (see review by Estes et al. 2011), and it is therefore a pressing management issue to understand the consequences of changing predator communities for the associated food webs and ecosystems.

## Box 1.3 Indirect effects of predation




**Keystone predation**: Species A indirectly increases species C through consumption of its competitor species B.

**Exploitative competition**: Species A indirectly affects species C by directly reducing the abundance of a shared resource species B.

**Apparent competition**: Increasing abundance of prey species A indirectly reduces the abundance of prey species C by increasing the abundance of the common predator species B.

**Trophic cascade**: Predator species A indirectly increases the abundance of species C by reducing the abundance of an intermediate species B that interacts with both species.

**Indirect commensalism**: Like indirect mutualism but with species A being more generalized in diet and feeding also on species C.

**Indirect mutualism with interference competition**: Species A indirectly increases the abundance of species D by reducing species B that is a competitive superior to species C that is a prey of species D.

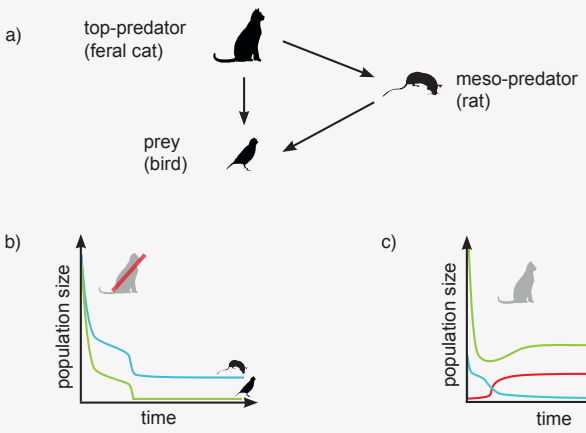
**Indirect mutualism with exploitative competition**: Species A indirectly affects species E through direct effects of their prey species B and D that share a common resource species C.

Solid lines indicate predation (arrows indicate direction of predation), dashed lines represent indirect competition.

Modified after Wootton 1994 and Menge 1995

## Box 1.4 Examples of indirect effects

### The feral cat example



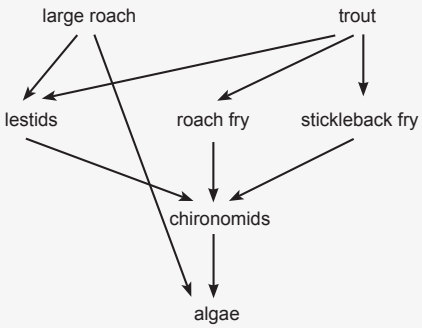

a) Introduced feral cats (top-predators) are a major threat of endemic bird species (prey) on many islands. The often considered solution in such cases is the eradication of the alien cats.

b) However, in a mathematical model, the removal of the cats even increased the threat to the birds through a meso-predator release of rats, another introduced species that have been allowed to spread on islands.

c) In the presence of the top-predator the rats were kept under control by the feral cats, but in their absence the rats drive the birds to extinction.

Modified after Courchamp et al. 1999

### The river food web example




Large predatory fish (roach and steelhead trout) reduced the abundance of predatory insects (lestids) and fish fry, thereby releasing their prey (chironomids) from predation pressure. The resulting higher densities of the grazing chironomids kept filamentous algae (*Cladophora*, epiphytic diatoms, *Nostoc*) at overall low biomass.

Modified after Power 1990

## "Are trophic cascades all wet?"

The concept of trophic cascades traces back to Hairston et al. (1960), who predicted a widespread importance of top-down control from carnivores on herbivores to producers in terrestrial ecosystems. These hypotheses were developed into a more general model describing the importance of system productivity for the strength of top-down control (Oksanen et al. 1981). Trophic cascades were first demonstrated for marine intertidal communities (Paine 1980), and later also in stream (Power et al. 1985, Power 1990) and lake ecosystems (Carpenter et al. 1985, Carpenter and Kitchell 1988). Until today, the most compelling examples of trophic cascades are derived from aquatic systems (see Shurin et al. 2002). Strong (1992) was the first to propose that trophic cascades should be restricted to low diversity systems, from which the majority are aquatic and have algae or lower plants at the base. Strong argued that algae and lower plants often lack defensive adaptations that are usually found in autotrophs (e.g. higher plants) of high diversity systems. Moreover, low diversity systems involve less heterogeneity and omnivory, which both can buffer strong consumer effects (Strong 1992). In contrast, high diversity systems are usually more complex and trophic cascades may rather appear as trophic trickles (Strong 1992).

Strong's hypotheses received much criticism and many of his arguments have been questioned. For instance, phytoplankton can possess diverse defence mechanisms similar to terrestrial plants (Smayda 1997, Ianora and Miralto 2010), omnivory is also very common in aquatic food webs (Diehl 1993), and the diversity of phytoplankton is high compared to plant communities (Duffy and Stachowicz 2006). Nevertheless, the major observation that most trophic cascades are more apparent in aquatic ecosystems holds (Borer et al. 2005) and the question remains: Are there major differences between terrestrial and aquatic systems, which could lead to fundamental differences between the food webs?

Most importantly, consumer control of producer biomass seems to be more significant in aquatic than in terrestrial systems (Polis 1999, Shurin et al. 2006). Aquatic herbivores can remove three times more producer biomass than terrestrial herbivores for a given primary productivity (Cyr and Pace 1993). The following characteristics were summarised by Polis (1999) and Shurin et al. (2006) and highlight the contrasts between aquatic and terrestrial systems.

1. Producer defence mechanisms limit their digestibility and therefore the consumption by herbivores. Chemical defences are known for producers in water and on land, but structural defences are more widespread in terrestrial plants, which produce skeletons from cellulose and lignin. Structural defences also exist in aquatic producers (e.g. phytoplankton), but are usually not as strong due to their need for buoyancy (Polis 1999).

2. Aquatic producers and herbivores have shorter life-cycles than the terrestrial counterparts, usually because they are smaller (Polis 1999, Shurin et al. 2006). A high growth rate and therefore a high turnover rate is a key mechanism for the cascading transfer of trophic effects.
3. Aquatic systems and specifically pelagic food webs are often size-structured (Shurin et al. 2006). Pelagic producers and herbivores are small due to the need for buoyancy and are generally killed by their consumers. In contrasts, the size ranges of terrestrial plants and herbivores can be very large, and therefore only certain life-stages are vulnerable to consumption or only parts of the plant are eaten (Polis 1999).
4. Nutrients become available to aquatic producers at a rate fast enough to sustain high levels of productivity (Polis 1999). First, turnover rates in the water are higher (see point 2) and second, the nutrient redistribution is faster in the water because of water movements, diffusion and mobile aquatic consumers (Polis 1999). At the same time, phytoplankton is almost entirely composed of nutrient-rich material (Shurin et al. 2006).

Other authors argue that trophic cascades are also common in terrestrial habitats (Chase 1998, Schmitz et al. 2000, Sinclair et al. 2000), and that there are more examples of aquatic trophic cascades simply because more studies have been done in aquatic systems (Chase 2000). In aquatic systems, fast-growing algae and small invertebrate consumers enable observations and experiments on smaller spatio-temporal scales, which may have contributed to an overrepresentation of aquatic cascade studies (Chase 2000). However, Polis (1999) differentiated between 'species cascades', where trophic levels consist of single species, and 'community-level cascades', where the trophic levels comprise entire communities. Trophic cascades that are found in terrestrial systems are accordingly often species-level cascades representing only a subset of the community (Polis et al. 2000). Community-level cascades are most likely to occur in systems that posses the following characteristics: (1) habitats are relatively homogeneous and discrete, (2) prey population dynamics are fast relative to the predator dynamics, (3) common prey are more or less uniformly edible, and (4) the systems are simple and trophically stratified with strong interactions between species (Polis et al. 2000). With these assumptions trophic cascades would be most likely in simple aquatic systems, for example in pelagic communities of lakes.

A meta-analysis of 54 lake experiments measuring the impact of planktivorous fish on zooplankton and phytoplankton revealed overall cascading effects (Brett and Goldman 1996). However, the phytoplankton response to the presence of planktivorous fish was highly skewed, and in two-thirds of the experiments the response was considered as weak (Brett and Goldman 1996). A meta-analysis of 102 experiments across six ecosystems (Shurin et al. 2002) revealed strongest trophic cascades in marine and lentic (lake and pond) benthos, and weakest cascades in marine plankton and terrestrial systems (Figure 1.1).

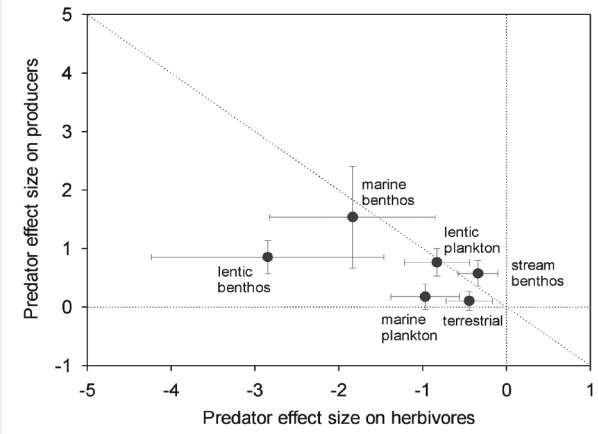



**Figure 1.1** Predator effect sizes on herbivores and producers in siy different ecosystems. The effect sizes were calculated as log ratios of herbivore and producer diversity in the presence of predators. Modified after Shurin et al. 2002.

Thus, trophic cascades in aquatic systems are indeed often stronger than in terrestrial systems. However, similarly large differences are found among different aquatic systems (Shurin et al. 2002, Borer et al. 2005), suggesting that within-system factors (like the above mentioned) are more important for the strength of a trophic cascade than general differences between aquatic and terrestrial systems (Shurin et al. 2002).

## Prerequisites and effectors of trophic cascades

The occurrence and strength of trophic cascades are determined by system-specific properties. Polis (1999) summarised three factors that should initiate and facilitate trophic cascades. First, trophic cascades depend on the appropriate extrinsic conditions. For example, the nutrient status is supposed to play a key role in triggering or suppressing a cascade (Sieben et al. 2011b). Second, only consumers and resources with key intrinsic characteristics (behavioural and life-history factors) are able to initiate cascading effects. For example, only the combination of efficient consumers on vulnerable but productive producers enables strong consumer effects. Third, resources that subsidise local consumers from channels outside the focal food web strengthen cascades. Such 'multichannel' resources, for example spatial or temporal subsidies or (life-history) omnivory, enable more consumers to survive in an area than possible through local resources.

Thus, both appropriate abiotic and biotic contexts are necessary to trigger a trophic cascade. Hereafter, I will give a brief overview about the empirical support for such effectors of trophic cascades.



**Diversity**

The importance of species diversity for the functioning of ecosystems has received increasing scientific attention, fuelled by the urgency to predict ecosystem consequences of species loss and species invasions. Species diversity embraces two main components: the number of species (richness) and the dominance structure of the species (evenness). It is important to not confuse species diversity and richness, since both are often used in the context of ecosystem functioning. At the simplest level, however, diversity can be synonymous with richness.

Modelling the effects of increasing producer richness on primary productivity gives an asymptotic relationship, where productivity increases strongly with increasing richness until it reaches 50% of the maximum productivity (Loreau 2000). Increasing species richness beyond that point has only minor positive effects on total productivity. These theoretical models have been shown to match quite well the relationships observed in grassland plant communities (Tilman et al. 1997a), where certain functional traits (e.g. the photosynthetic pathway and the nitrogen fixation) are responsible for a positive richness response. Furthermore, a similar relationship was shown for consumers, where higher herbivore diversity enhanced secondary production (Duffy et al. 2003).

Generally, two mechanisms are responsible for diversity effects on ecosystem functioning. First, complementary properties of species (niche partitioning or facilitation) can lead to species mixtures that show higher response than the best-performing monoculture (Loreau and Hector 2001). Second, higher diversity increases the likelihood of including a highly productive species and therefore, the species mixture is performing as well as the best monoculture (Tilman et al. 1997b). The latter sampling effect assumes that the most productive species also dominates the community. Since this assumption is not always met, the sampling effect was later generalised as the selection effect (Loreau and Hector 2001), where the dominant species in a mixture can perform better or worse compared to the respective monoculture. Different empirical studies that have partitioned the two types of diversity effects (Loreau and Hector 2001) have found positive complementarity (likely due to resource partitioning) and negative selection effects (the most productive species is not the dominant) (Bruno et al. 2005, Reusch et al. 2005). Interestingly, negative selection effects that are negating positive complementary effects were found frequently in marine benthic communities (in Stachowicz et al. 2007). However, partitioning the diversity effects is laborious because the specific contribution of each species in a mixture has to be determined (Stachowicz et al. 2007).

In a food web perspective, we distinguish the diversity within one trophic level from the diversity of trophic levels (horizontal and vertical diversity, respsectively; *sensu* Duffy et al. 2007). Traditionally, research on the effects of diversity on ecosystem processes focused on horizontal diversity, by studying effects of diversity or richness of species or species groups within one trophic level. More recently, studies also address vertical diversity, by

testing effects of e.g. the degree of omnivory in food webs or the food chain length (e.g. Duffy et al. 2007). A meta-analysis from studies on grazer-algae-interactions found that higher producer diversity reduced predation effects (Hillebrand and Cardinale 2004), probably due to (i) a higher chance of including inedible species (edibility hypothesis) and (ii) the reduced efficiency of specialist predators confronted with diverse prey (dilution hypothesis) (*sensu* Duffy et al. 2007). Further, higher herbivore diversity increases herbivore biomass but has almost no effect on producer biomass (meta-anlysis by Balvanera et al. 2006) or a negative effect on producers (meta-analysis by Cardinale et al. 2006).

In systems with strong top-down control, ecosystem properties are most strongly affected by changing predator diversity (Reiss et al. 2009). However, predator diversity effects are especially difficult to generalise because of highly variable interspecific interactions among predators (Douglass et al. 2008). Higher predator diversity can either increase or decrease the impact on prey, and accordingly reduce or enhance the impact on producers. The sign and strength of this effect depend on e.g. the degree of omnivory, intraguild predation, diet complementarity and prey behaviour (Finke and Denno 2004, Bruno and O'Connor 2005, Byrnes et al. 2006, Duffy et al. 2007, Stachowicz et al. 2007). Furthermore, high predator diversity can decrease the likelihood of trophic cascades through emerging trait-mediated interactions (for example predator avoidance mechanisms of the prey including reduced (grazing) activity) (O'Gorman et al. 2008).

However, diversity effects consider the performance of a polyculture compared to the average monoculture and thereby ignore the composition of a species assemblage (at equal species number). Individual species differ in their effects on ecosystem processes and therefore determine the performance of a species assemblage (Worm and Duffy 2003, Stachowicz et al. 2007). These composition or idiosyncratic effects were found in several diversity studies and in studies that compared both effects, idiosyncratic effects were often of a larger magnitude than richness effects (Stachowicz et al. 2007). Experiments by Duffy and others suggest that effects of species loss will be more idiosyncratic when diversity is initially low (Duffy et al. 2001, Duffy et al. 2003, O'Connor and Crowe 2005, Stachowicz et al. 2007). Furthermore, several food web properties are suggested to change with diversity, such as the overall number of links, the number of links per species and the mean and maximum length of food chains (Hillebrand and Shurin 2005).

In conclusion, the effects of species diversity on the food web composition depend on several factors, for example the initial diversity, the focal trophic level, the ecological role of the species, and food web properties such as connectedness and interaction strength. Furthermore, extrinsic factors such as the nutrient status of the system regulate diversity effects.

**Omnivory**

Omnivores can be defined as organisms that either consume animals and plants, or feed from more than one trophic level. In accordance with the latter definition from Pimm and Lawton (1978), special cases of omnivory include intraguild predators and life-history omnivores. Intraguild predators feed on their own and the next lower trophic level and life-history omnivores are feeding on different trophic levels during their different life

stages (Duffy et al. 2007). Such life-history omnivory is often accompanied with an ontogenetic habitat shift and can be either discontinuous (metamorphosis) or continuous with growth (Polis and Strong 1996). Early studies suggested that omnivory is rare in nature, and early models showed that omnivory would destabilise food webs (Pimm and Rice 1987). In fact, omnivory is ubiquitous in (aquatic) food webs (Diehl 1993, Polis and Strong 1996) and more recent models indicate that omnivory can locally stabilise the food web (Fagan 1997, McCann and Hastings 1997, Neutel et al. 2002). Omnivory affects the food web structure and energy flow in various ways. First, omnivory dilutes consumptive effects and therefore buffers consumer control from propagating down the food web (Polis and Strong 1996). Second, omnivory short-circuits food chains by shunting the energy flow to non-adjacent trophic levels (Polis and Strong 1996). Third, omnivory increases food web complexity (Polis 1991) and therefore decreases predictability.

Several recent studies addressed the role of omnivory in food webs specifically to predict ecological consequences of species loss or diversity decline. A model study showed that omnivory can buffer effect of species loss (Petchey et al. 2004), and experiments showed that higher predator diversity decreased producers when omnivores and intraguild predators were added to the predator community (Bruno and O'Connor 2005, Finke and Denno 2005).

In conclusion, omnivores short-circuit food chains and therefore increase food web complexity. Furthermore, omnivores may hamper the initiation of trophic cascades by feeding from two trophic levels, which could stabilise food webs.

**Nutrients**

Nutrients determine primary productivity and have therefore fundamental control over higher trophic levels (Power 1992). Low nutrient availability cause large parts of the open oceans to be "blue deserts" with exception of upwelling zones (Polis 1999). Coastal zones are mainly supplied with nutrients through rivers and run-offs from land. Higher nutrient availability increases producer biomass and changes producer stoichiometry and community composition (Hillebrand and Kahlert 2001, Gruner et al. 2008). However, relative effects of nutrient enrichment depend on the nutrient status of the system (Lotze et al. 2001). In systems with low productivity, nutrient enrichment may enhance diversity by allowing rare species to accumulate (Hillebrand et al. 2007), whereas in systems with a high productivity additional nutrients may decline diversity by favouring one or a few producer species (Hillebrand and Sommer 1997). In an experiment that evaluated the relationship between resource availability and macroalgal diversity, Bracken and Nielsen (2004) found that local nutrient additions increased producer diversity but only up to nutrient levels that were typical in the respective system. Resource enrichment beyond the normal levels reduced producer diversity. Furthermore, nutrient effects on producers depend on their species composition and habitat structure. Specifically, the presence of (canopy-forming) macroalgae inhibits the positive nutrient effects on understory foliose and turf-forming algae (Russell and Connell 2005, Eriksson et al. 2006a,b).

Herbivores can substantially reduce producer biomass and therefore have the potential to dampen positive nutrient effects (Hillebrand et al. 2000). Furthermore, herbivores can increase producer evenness through the removal of dominating species, and thereby

counteract nutrient enrichment that otherwise decreases producer evenness through higher dominance of a few species (Hillebrand 2003). However, nutrient effects on producers also interact with consumer control by herbivores (Proulx and Mazumder 1998, Worm et al. 2002, Gruner et al. 2008). Russell and Connell (2007) showed that, when rocky shores herbivores were exposed to higher nutrient loads, they removed more biomass of algae. However, the herbivores could not counteract the increased algal growth over a longer period. In other studies however, herbivores controlled effects of nutrient enrichment on rocky shore algae (Lotze et al. 2001, Worm et al. 2002), which suggests a system- and context-specific relationship of nutrient and herbivore effects on producers (but see Hillebrand et al. 2007).

Theory also suggests that high nutrient availability initiates and promotes trophic cascades (Leibold 1989, Polis 1999). Field studies in aquatic (e.g. Moksnes et al. 2008, Eriksson et al. 2009, Sieben et al. 2011a,b) and terrestrial (e.g. Sinclair et al. 2000, Elmhagen and Rushton 2007) systems support that a high primary productivity positively affects the strength of trophic cascades. However, field studies also showed that effects of predation and productivity depend strongly on the diet breadth of the herbivores (Leibold 1989) and on their functional composition (Råberg and Kautsky 2007b, Sieben et al. 2011b). Accordingly, a meta-analysis of predator removal experiments suggests that system productivity affects only producers and that the strength of trophic cascades rather depends on consumer traits (Borer et al. 2005). Nutrient effects are usually of a larger magnitude than predator effects on producers, but bottom-up effects (nutrients - herbivores) attenuate more rapidly than top-down effects (predator – producer) (Borer et al. 2006). Meta-analyses of trophic cascades by Borer et al. (2005, 2006) and Shurin et al. (2002) (see Figure 1.1) indicate that the plant-herbivore link is critical for the transition of both top-down and bottom-up effects, indicating a strong dependence of consumer effects (depending on consumer traits) and nutrient availability in food webs.

In conclusion, the nutrient status of an ecosystem increases the primary production, affects the species composition of the producers and may have strong effects on the food web composition. The effects of a nutrient input depend on the initial nutrient status, the species composition of the producers, the concomitant grazing pressure, as well as the composition of higher trophic levels.

**Spatial and temporal subsidies**

Ecosystems are usually open and temporally as well as spatially heterogeneous. Trophic linkages across ecosystems (littoral/sublittoral or land/water), so-called spatial subsidies, are common. Nutrients (e.g. run-off or up-welling), detritus (e.g. leaf fall into water), prey or consumers (migrate or forage across habitats) frequently cross habitats from the donor to the recipient system (Polis and Strong 1996). Large amounts of biomass are transported through large-scale ecosystem coupling processes. A temporal subsidy is for example food that is left from previous pulses of productivity (Polis 1999).

Generally, subsidies of nutrients increase primary productivity and subsidies of detritus or prey produce numerical responses in their consumers (Polis and Strong 1996). For example, the pelagic-benthic coupling is one major route for nutrients and detritus (Graf 1992) as well for certain life-stages of many benthic and planktonic organisms (Marcus

and Boero 1998); migrating fish transport large amounts of nutrients and energy from marine systems into lakes (Durbin et al. 1979) or from the ocean to the coast (Varpe et al. 2005); drifting kelp from distant reefs is an important resource for sea urchins (Vanderklift and Wernberg 2008). Migrations of predators have the potential to initiate trophic cascades in the receiving food webs (Guidetti 2007, see also Eriksson et al. 2011) while prey subsidies allow local predators to be more abundant than if supported only by local resources, which may initiate or strengthen trophic cascades (Polis 1999).

Several studies suggest that subsidies have strongest effects where the differences between donor and recipient habitat productivity are large (magnitude of the subsidy; e.g. Polis et al. 1997). A recent model analysis showed that ecosystems with high amounts of allochthonous input would experience stronger cascades than systems with low allochthonous inputs (Leroux and Loreau 2008). The same model also predicted that inputs at predator and producer level would result in larger cascading interactions (Leroux and Loreau 2008). Therefore, the trophic position at which the subsidy enters the food web will determine the effect on the recipient system. A study of land-to-sea subsidies on a rocky coast found that higher magnitudes of subsidy shift the habitat from more perennial algae to more ephemeral algae (Gorman et al. 2009). A meta-analysis of 32 studies (marine, limnic and terrestrial) revealed several general patterns across systems (Marczak et al. 2007). First, the magnitude of response to the subsidy does not depend on the ratio of donor and recipient productivity (Marczak et al. 2007). Second, the magnitude of response to the subsidy depends on the structure of the recipient habitat. Subsidies have strongest effects in recipient systems that are relatively open to neighbouring systems such as coastal habitats (Marczak et al. 2007). Third, trophic levels respond differently to subsidies. The response of lower trophic levels (herbivores and detrivores) to subsidies is almost twice that of the predators (Marczak et al. 2007).

In conclusion, temporal and spatial subsidies are common, may have strong effects on the recipient system and even induce a habitat shift. The food web effects of subsidies depend on the structure of the recipient system (e.g. the openness) and the recipient trophic level, whereas effects of the magnitude of the subsidy are equivocal.

## Anthropogenic effects on trophic cascades

Human activities and the extensive use of the environment have induced severe global changes. Biogeochemical cycles are altered through the extensive use of industrial fertilizer in agriculture leading to increasing nutrient loads of estuaries and coastal zones, increasing water consumption and the continuous production of greenhouse gases (Chapin et al. 2000). Since the beginning of the industrial revolution, humans have transformed 40-50% of the ice-free land surface and increased the concentration of atmospheric $CO_2$ by 30% (Chapin et al. 2000). Today, we use more than half of all accessible surface fresh water, dominate one-third of the net primary productivity on land and drive species invasions through the high mobility of people (Vitousek et al. 1997, Chapin et al. 2000). All together, these rapid and mostly irreversible changes of the global environment have severely altered biological diversity and triggered the sixth major extinction event in the history of life (Chapin et al. 2000). The biodiversity of an ecosystem affects the goods and services that it provides. Accordingly, a decline in biodiversity will influence human economic and social activities. Indicators of the state of biodiversity show continuous declines, whereas indicators of the pressures on biodiversity show still increases (Butchart et al. 2010). Despite the extensive but incomplete knowledge about the causes and likely consequences of further biodiversity loss, environmental resources are still used in an unsustainable way.

Human activities affecting marine systems include: commercial fishing, shipping, coastal and offshore engineering (e.g. oil platforms, offshore wind parks, sediment extraction) and urban and agricultural activities. Altogether these activities cause an input of nutrients and pollutants, habitat destruction and fragmentation, as well as direct and indirect changes of species communities (Halpern et al. 2008). Furthermore, these effects may have unpredictable synergistic effects with effects of climate change: including ocean acidification, rise in sea temperature and sea level and increased UV-B radiation. Today, there are no areas unaffected by human influence, and 41% of the marine systems are strongly affected by multiple anthropogenic drivers (Halpern et al. 2008). Areas of low impact remain only in some parts of the open oceans (mainly in the Southern hemisphere) and near the poles, where seasonal or permanent ice coverage is limiting human access (Halpern et al. 2008).

Commercial fishing and nutrient inputs are among the globally widespread anthropogenic impacts that have a direct link to marine food web structure. As part of this thesis I investigate consequences of both overexploitation (as the loss of top-predators) and eutrophication (from nutrient input) for the composition and stability of food webs and how this influences the occurrence and strength of trophic cascades. Therefore, I will briefly introduce both anthropogenic impacts and give some examples.

### Fisheries

Commercial fishing is historically one of the most important and destructive human impacts on marine ecosystems. Large vertebrates were ubiquitous for millions of years in marine ecosystems (Estes et al. 2011). Sea turtles, whales, manatees, dugongs, sea cows, monk seals, crocodiles, codfish, jewfish, swordfish, sharks and rays are now functionally or

entirely extinct in most coastal ecosystems (Jackson et al. 2001 and references therein). About 90,000 year ago, when people learned how to fish, many large consumer species already started to decline. Overfishing of large vertebrates and shellfish was the first major anthropogenic impact and preceded all other natural and human disturbances to coastal ecosystems, such as pollution, habitat fragmentation and climate change (Jackson et al. 2001). Three simple patterns regularly occur together with overfishing (see also Box 1.1): a decrease in the average size of the fish species, a decrease in the average age of the fish species and a decrease in the relative abundance of super-spawners (Sala and Sugihara 2005). Overfishing also induces evolutionary changes such as maturation at smaller size and lower age as well as increased fecundity, which can be observed in decadal time scales (Jørgensen et al. 2007). Such rapid evolutionary changes depend on the harvest rate and the harvest method (e.g. size-selectivity of fishing gear) (Palkovacs 2011).

Another consequence of size-selective fishing may be the decline of the overall mean trophic level (MTL) in fisheries landings because of mainly targeting large species (Pauly et al. 1998). The so-called 'fishing down the food web' stands for a gradual transition of the target species from long-lived, high trophic level, piscivorous bottom fish towards short-lived, low trophic level invertebrates and planktivorous pelagic fish (Pauly et al. 1998, Pauly and Palomares 2005, Pauly et al. 2005). Later it has been suggested that the common underlying mechanism for the observed decline in MTL, is a sequential addition of low-trophic-level fisheries, rather than the replacement of high- by low-trophic-level fisheries ('fishing through marine food webs' *sensu* Essington et al. 2006). However, the decline in MTL of global catches is highly controversial. MTL from surveys and assessment often diverge from catch MTL (Branch et al. 2010). Thus, the widely used marine indicator 'catch MTL' may not reliably predict changes in marine ecosystems (Branch et al. 2010). Accordingly, a recent analysis of fisheries datasets found that populations of small, low-trophic-level species collapsed just as often as populations of large predators (Pinsky et al. 2011).

Since most marine apex consumers are under strong pressure from human exploitation, the role of overfishing for changes in top-down control and trophic cascades receive more and more scientific attention. However, the demonstration of cascading impacts from overfishing is difficult because many populations have been reduced since decades or even centuries (Dayton et al. 1998). Along with these missing baselines comes the problem that trophic interactions must be perturbed in order to detect cascades, and even then cascading reactions may be delayed by years or decades (Estes et al. 2011). Despite these challenges, there are a number of well-supported studies identifying fishing as the main trigger for observed cascades.

*Example 1.* Hunting or fishing on predators of sea urchins have been connected to strong increases in sea urchins and a subsequent deforestation of kelp forests (Pinnegar et al. 2000). In the Northern Pacific (Aleutian Islands, Alaska) the respective predators were sea otters. Islands without sea otters possessed higher densities of sea urchins and low abundances of kelp; whereas at sites with sea otters present, kelp was abundant and urchin densities were lower (Estes and Palmisano 1974, Estes et al. 1978, Pinnegar et al. 2000). The decline in sea otters before the 20$^{th}$ century was mainly attributed to hunting, whilst

later an increasing predation by killer whales was hypothesized due to declines of the whales' primary prey (sea lions) (Estes et al. 1998).

*Example 2.* In the Gulf of Maine, declines in large predatory groundfish (mainly cod) are connected to declines in kelp abundance. Today, large groundfish are functionally absent and abundances of benthic invertebrates (sea urchins, lobsters and crabs) have increased. Accordingly, kelp abundance is significantly lower in the Gulf of Maine compared to sites dominated by large predatory fish that prey on the urchins (Steneck et al. 1995 from Pinnegar et al. 2000).

*Example 3.* In the Mediterranean, the depletion of sea urchin's predators is assumed to be a main factor in shifting the Mediterranean rocky sublittoral between the 'developed' fleshy erect algae community-state and the overgrazed community with high densities of sea urchins and coralline barrens (Sala et al. 1998, Pinnegar et al. 2000). The abundances of large predatory fish have been shown to be higher within Marine Protected Areas (MPAs) compared to outside, particularly of those fish species predating on different life stages of a common sea urchin species (Sala 1997). When sea urchins occur at high densities such as outside the MPAs, they can deplete large erect algae and induce the formation of coralline barrens (Pinnegar et al. 2000 and references therein).

*Example 4.* In the Caribbean, a substantial shift from hard-coral to macroalgal domination occurred in the 1980s that was attributed to overfishing of both large predatory fish and grazing fish (Hughes 1994, Pinnegar et al. 2000). The decline in abundances of sea urchins' predators as well as competitors enabled a single urchin species to dominate the herbivorous community until a pathogen induced their mass-mortality (Lessios et al. 1984). Accordingly, fast-growing macroalgae were not controlled by the urchins anymore and could overgrow coral reefs.

Thus, apart from the risks of ecological extinction of entire trophic levels and the induction of trophic cascades, fisheries exploitation has also community-wide effects that are transferred through the food web. First, fishing removes the slow growing species first and thereby acts the opposite way as ecological succession where the average growth rate decreases with increasing successional stage (Margalef 1968). Fishing therefore accelerates the turnover of food webs, which might increase ecosystem productivity. However, a clear relationship between the degree of exploitation and ecosystem productivity, which is a necessary prerequisite for most ecosystem management approaches, is lacking. Accelerated growth rates also show higher fluctuations, which can destabilize systems similar to resource enrichment (May 1974 from Sala and Sugihara 2005).

Second, fishing is likely to remove strong food web interactors first (Bascompte et al. 2005). Following the definition of Paine (1992), strong interactors are species that are capable of preventing the development of a prey monoculture or of destroying one already established in the absence of their enemies. The selective depletion of the strongest interactors can therefore increase the likelihood of propagating trophic cascades depending on the complexity and connectivity of the food web.

Third, food webs generally exhibit greater complexity in the presence of marine top-predators than in their absence (Sala et al. 1998). Most marine fish species are generalists with few trophic specialists (Link 2002). The emerging high connectivity suggests that marine food webs could be more resistant to trophic cascades in the presence of top-predators (Sala and Sugihara 2005). Apart from effects on the food web, losing apex consumers can have further indirect and often unanticipated effects of on processes such as diseases, carbon sequestration, invasive species and biogeochemical cycles (Estes et al. 2011).

The oceans provide 16% of the animal protein to humans worldwide - that is 17.1 kg fish per capita worldwide (FAO 2008). This underpins the importance of sustaining the goods from the sea. However, fisheries management has so far proved to be a failure, with overexploitation being the rule rather than the exception (Peterson and Estes 2001). The ecological extinction of entire trophic levels and the concomitant fishing down or through the food web are a clear evidence of unsustainable management.

**Eutrophication**

Human activities mobilise and enhance the availability of nitrogen (N) and phosphorus (P) through land clearance, forestry, agriculture, application of fertilizer, discharge of human waste, animal production and combustion of fossil fuels, which is leading to elevated nutrient levels in ground and surface waters (Cloern 2001). As a consequence, nitrogen and phosphorus inputs into the oceans increased by almost five and three times, respectively, during the 20$^{th}$ century (Smith et al. 1999, Steffen et al. 2007). Primary productivity is commonly nutrient-limited and phytoplankton biomass has, therefore, increased with increasing nutrient concentrations, especially in coastal ecosystems (Cloern 2001). Furthermore, eutrophication has large effects on the species richness and composition of phytoplankton. Whether nutrient enrichment increases or decreases producer richness depends on the productivity of the ecosystem (see pages 22-23). Concerning changes in species composition, more extensive summer blooms of inedible algae (e.g. *Phaeocystis* spp., toxic dinoflagellates) have been measured as well as decreases of diatoms (Cadée 1982 in Brockmann et al. 1990, Sommer et al. 2002 and references therein). High phytoplankton biomass decreases the water transparency and therefore indirectly limits the habitat for benthic producers (Cloern 2001). For example in the Baltic Sea, the depth penetration of the bladderwrack *Fucus vesiculosus* L. (hereafter *Fucus*) decreased from a lower limit of 11.5 m in the 1940s to 8.5 m in the 1980-90s, which has been attributed to a decrease in water transparency (Kautsky et al. 1986, Eriksson et al. 1998).

According to the changes in phytoplankton, nutrient enrichment strongly influences the community composition of benthic producers. Slow-growing vascular plants or perennial macroalgae are often replaced by fast-growing microalgae or ephemeral macroalgae that respond more quickly to nutrient pulses (Duarte 1995). These shifts in producer communities can have detrimental effects on animal communities. For example, *Fucus* provides habitat for diverse invertebrate communities, and in the Baltic Sea it was shown that the associated fauna had generally higher biomass and abundance at sites with intact *Fucus* vegetation compared to those where *Fucus* has disappeared (Wikström and

Kautsky 2007). Prevailing colonisation of epiphytes on perennial macroalgae can be harmful for such habitat-forming species because both compete for the same resources, light and nutrients (Korpinen et al. 2007a). Eutrophication increases the growth of epiphytes and therefore acts as a main threat for assemblages of perennial macroalgae such as seagrass or *Fucus* beds (Wear et al. 1999). However, high primary productivity can also increase the secondary production. For example, the macrozoobenthos biomass showed trends of increase, whereas the mean size decreased, with higher biomass of phytoplankton and microphytobenthos in the Dutch Wadden Sea from 1970 to 1990 (Beukema 1991).

Furthermore, enhanced primary production affects sediment conditions and benthic communities when phytoplankton sinks to the bottom where it is deposited. Enhanced deposition of organic material stimulates benthic microbial activity and the consumption of dissolved oxygen in bottom waters with often dramatic effects on benthic communities (Diaz and Rosenberg 2008). Sedimentation also decreases macroalgal recruitment success and changes algal community composition (Eriksson et al. 1998, Eriksson and Johansson 2005). Additionally, increased primary production may also favour invertebrate grazing rates (e.g. Worm et al. 2002, Hillebrand 2003, see pages 22-23).

Ecosystem changes due to eutrophication are often reversible. However, some systems experience multiple impacts and their cumulative and indirect effects impair the ability to predict and manage those systems (Lotze and Milewski 2004).

## 2. THE BALTIC SEA



The Baltic Sea is a brackish semi-enclosed sea that sequentially drains into the Kattegat, the Skagerrak and the North Sea. The narrowest and shallowest passages into open waters are the Darß Sill (18 m deep), the Sound (7 m) and the Danish straits (up to 80 m) before entering the Kattegat. Together, they form the transition zone between the Baltic Sea and the North Sea. The Baltic Sea covers an area of 415,266 $km^2$ and with a volume of approximately 21,000 $km^3$, is one of the largest bodies of brackish water. The average depth is 55 m and the maximum depth is 459 m (Landsort Deep, Eastern Gotland Basin). Nine bordering countries form 8,000 km of coastline. The bordering countries plus five non-bordering countries make a total catchment area of 1,745,100 $km^2$ (Figure 1.3), which is 4.3 times the area of the Baltic Sea. The largest rivers discharging into the Baltic Sea are the Neva (into the Gulf of Finland) and the Vistula (into the Baltic Proper). About 85 million people inhabit the Baltic Sea catchment area, of which 40 million live in the coastal zone (see references in: Voipio 1981, Snoeijs 1999, Schliewer 2008).

The formation of the Baltic Sea began after the last glaciation about 12,000 years ago and hence is a relatively young sea. The present salinity conditions were established only 3,000 years ago. The Darß Sill, as a border between the Western Baltic Sea and the adjacent Baltic Basin, together with the Sound inhibit water exchange with the North Sea. The inflow and outflow events are strongly dependent on salinity differences. Only high salinity (heavy) water can enter the Baltic Sea as a sub-surface layer, while lower salinity (light) surface water is discharged into the North Sea. The annual water volume leaving the Baltic Sea is more than the double of the water volume that enters the Baltic. This difference is compensated by freshwater run-off from rivers. The high inflow of freshwater together with the special topographical structure of the Baltic Sea and particularly the Belt Sea, cause a permanent halocline in the Baltic Sea with low salinity surface water (7-8 PSU) and high salinity bottom water below 60 m (9-20 PSU). This layer hinders or prevents ventilation and oxygenation and cuts deep basins off from oxygen supply. Consequently, oxygen depleted zones are formed in the deeper parts mainly in the central Baltic Proper. In the last decades, eutrophication has significantly promoted and enlarged these zones (Jonsson et al. 1990).

The hydrographic regime and a north-south extension of more than 1,200 km cause a salinity gradient from the Skagerrak (20-30 PSU), over the central Baltic Proper (7-13 PSU) to the Gulf of Bothnia (2-4 PSU). Similarly, the Baltic Sea shows a temperature gradient that is substantially influenced by the duration of the ice coverage that decreases from north to south (Ojaveer et al. 2010). The Baltic Sea is virtually non-tidal (the average tidal amplitude is 15 cm), with exception of the North Sea-influenced Kattegat. Differences in water level are instead mainly due to changes in air pressure and wind. These stagnant conditions (especially in deep waters) cause a long water-turnover time of approximately 33 years (see references in Voipio 1981, Snoeijs 1999, Schliewer 2008).

Its hydrographic regime and the short geological history are the main reasons of the Baltic Sea's low species diversity. Overall, there are more marine than freshwater species in the Baltic Sea because the physiological adaptation to brackish conditions is easier for marine species due to the brackish water ion composition that is more similar to marine

water. The salinity at which only a minimum of both marine and freshwater species can exist ("horohalinikum") is at 6-8 PSU. Therefore, total species numbers are lowest in the Baltic Proper. From south to north and in inshore waters, the number of marine species decreases and freshwater species increase (Figure 1.2). This decline in species diversity with decreasing salinity was shown particularly for zoobenthos (Remane 1955, updated in: Ojaveer et al. 2010) and phytobenthos (Snoeijs 1999). Consequently, food webs are relatively simple, which makes them more susceptible to external perturbations (Sokołowski et al. 2012).

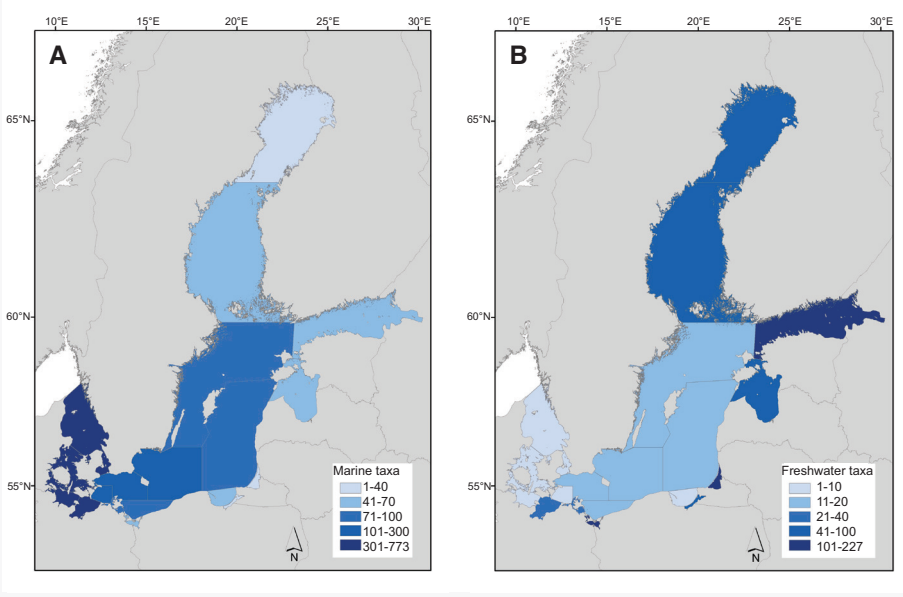



**Figure 1.2** Distribution of macrozoobenthic species of (A) marine and (B) freshwater origin in the Baltic Sea. Modified after Ojaveer et al. 2010.

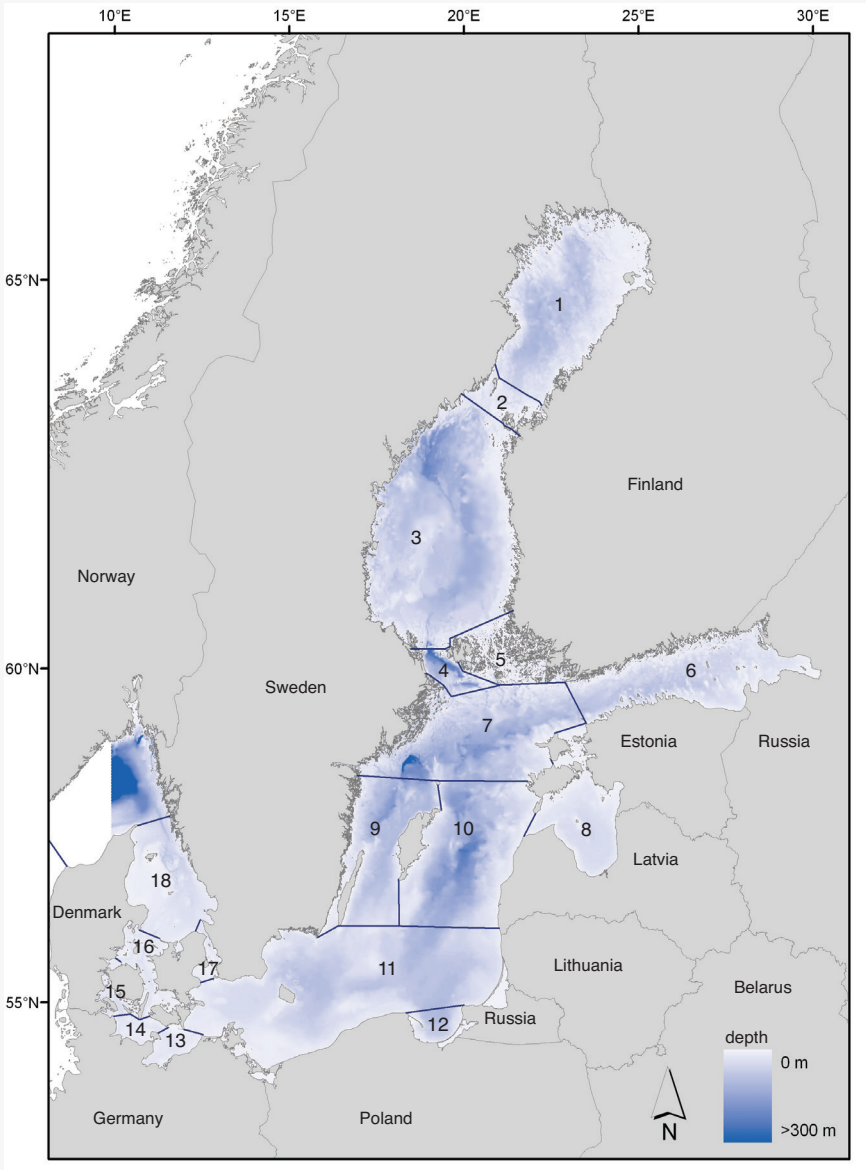



**Figure 1.3** Baltic Sea with the nine bordering countries and sub-basins as defined in the HELCOM COMBINE manual (http://www.helcom.fi/groups/monas/CombineManual/PartA/en_GB/main/). (1) Bothnian Bay; (2) The Quark; (3) Bothnian Sea; (4) Åland Sea; (5) Archipelago Sea; (6) Gulf of Bothnia; (7) Northern Baltic Proper; (8) Gulf of Riga; (9) Western Gotland Basin; (10) Eastern Gotland Basin; (11) Southern Baltic Proper; (12) The Gulf of Gdansk; (13) Bay of Mecklenburg; (14) Kiel Bay; (15) Little Belt; (16) Great Belt; (17) The Sound; (18) Kattegat.

## Anthropogenic effects on trophic cascades

The special topographical structure of the Baltic Sea strongly limits the exchange with open waters. As a result, the water column shows permanent (thermohaline) stratification with an average residence time of the water body in the Baltic of 33 years (Schliewer 2008), which makes most parts of the Baltic Sea particularly sensitive to natural or human-induced disturbances.

**Eutrophication**

The Baltic Sea is impacted by an excess input of nutrients that have had severe effects on environmental conditions and the biological community (Jansson and Dahlberg 1999). In the past decades, a several-fold increase in nutrient loads (Elmgren 1989) resulted in an increase in spring phytoplankton biomass and cyanobacterial blooms in the central Baltic (Cederwall and Elmgren 1990, Kahru et al. 1994, Wasmund et al. 1998), a decrease in water transparency (Sandén and Håkansson 1996) and a 5 to 10-fold increase in sedimentation of organic matter (Jonsson and Carman 1994) in the open Baltic Proper. At the same time, increasing problems in coastal zones are reported: the excessive growth of filamentous algae, which can eventually form drifting algal mats (Vahteri et al. 2000, Bonsdorff et al. 2002), a decreased depth penetration of the benthic vegetation due to decreased light penetration and increased sedimentation of organic matter (Kautsky et al. 1986, Eriksson et al. 1998, Eriksson and Johansson 2003) and a shift in species composition of flora and fauna (Jansson and Dahlberg 1999).

Most parts of the Baltic Sea are affected by eutrophication: 161 out of 172 examined coastal areas are affected by high nutrient loads, most of which are classified as to be in a poor or bad condition (HELCOM 2009). 75% of the nitrogen load to the Baltic Sea comes from rivers within the catchment area, of which 80% originate from agriculture. 95% of the phosphorous enters mainly via point sources (e.g. wastewater effluent) of which 90% come from municipalities. The nutrients, once discharged to the Baltic, will remain for many years because of the limited water renewal. Regarding the open waters, only the Bothnian Bay and the northeastern Kattegat are not considered to be eutrophied, probably because of the higher water exchange (HELCOM 2009). However, the nutrient status varies greatly over the different sub-basins. While the Bothnian Bay and the Bothnian Sea have mostly close to pristine conditions with low levels of phosphorous, low summer chlorophyll-*a* and a high water transparency; the Baltic Proper, Gulf of Finland, Gulf of Riga, Gulf of Gdansk and the Gotland Basin are most strongly affected by eutrophication (to at least 50% in a bad condition) (HELCOM 2009). Nutrient concentrations in the Baltic have increased until the 1980s; subsequently, the nutrient load, particularly from municipal and industrial sources, has significantly decreased. However, the nutrient concentration is still high, particularly total nitrogen, which has remained unchanged in the last 20 years (HELCOM 2009). Furthermore, the emissions from agriculture seem to be difficult to dampen (HELCOM 2011). Recent simulations of the Baltic Sea hydrographical-biogeochemical cycles (see also Box 1.2) have shown that all efforts to reduce the nutrient input taken so far resulted in maintaining the status quo only

and that "additional action is needed in order to improve water quality" (Gustafsson et al. 2012).



## Fisheries

Fisheries have drastically changed the food web structure in the Baltic Sea. The total fish catch in the Baltic Sea increased 5- to 10-fold during the last century, but has decreased again since the mid 1990s. Today, three species, *Gadus morhua* L (Atlantic cod), *Sprattus sprattus* (L) (European sprat) and *Clupea harengus* L (Atlantic herring) (Figure 1.4) comprise 95% of the total catch (ICES 2009).

Fishing for **cod** increased from the mid 1970s and peaked in 1984 when 22% of the global catch of cod originated in the Baltic Sea (Österblom et al. 2007). Since then, cod catches declined strongly until 1990 with no tendency to recover (Casini et al. 2008). Additional to high fishing pressure, cod reproduction is restricted to a few deep areas where the salinity is sufficiently high (> 10 PSU). High productivity, and therefore high organic load sinking to the bottom, often leads to oxygen deficiency in these deep waters. Cod eggs are particularly sensitive to low oxygen levels (Köster et al. 2003), but also adult cod can be negatively affected by high nutrient loads in coastal areas (Hansson and Rudstam 1990). Most importantly, there is no other top-predator in the open water system that could replace cod on the top of the food web.

**Sprat** catches were high from the mid 1950s until 1970, which was suggested to be partly a result of eutrophication (Hansson and Rudstam 1990). From 1970 sprat strongly decreased probably due to a combination of fishing and heavy predation by a large cod stock (Hansson and Rudstam 1990). Since the mid 1990s sprat catches increased again,

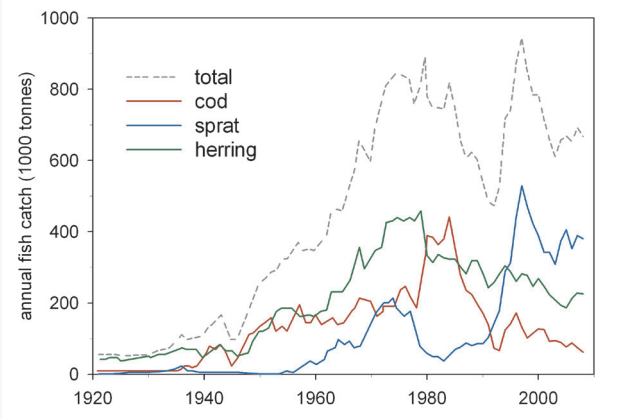



**Figure 1.4** Catches of *Clupea harengus* (herring, green line), *Gadus morhua* (cod, red line), and *Sprattus sprattus* (sprat, blue line) compared to total catches (black line) from 1920 to 2010 in the Baltic Sea (ICES subdivision 22-32). Data from ICES 2009 and Hansson and Rudstam 1990.

following the strong decline in cod stocks, which released sprat from predation pressure (Casini et al. 2008).
Fishing on **herring** increased until the 1980s. Some authors suggested that these high fishing yields were, similar to sprat, at least partly due to eutrophication (e.g. Otterlind 1976 in Hansson and Rudstam 1990). The higher primary production could fuel zooplankton biomass, the main food source for herring larvae. However, eutrophication may also have a negative impact on adult herring through negative effects on their benthic diet (e.g. amphipods or mysids) (Kostrichkina and Oyaveyer 1982 in Hansson and Rudstam 1990).

A recent study calculating impact indices of several anthropogenic pressures identified fishing as a high pressure on the ecosystem in all areas of the Baltic Sea (Korpinen et al. 2012). Highest impact values occurred in the southern parts of the Baltic (Arkona Basin, Bornholm Basin, Eastern Gotland Basin and Kattegat). Specifically, stocks of cod and herring are below safe biological thresholds due to overfishing (Korpinen et al. 2012), but also due to climatic changes in salinity and oxygen concentrations (ICES 2007 in Korpinen et al. 2012).

There are strong indications that the dramatic changes in higher trophic levels by fishing have caused a trophic cascade and thereby influenced the lower trophic levels in the open Baltic Sea. A food web analysis over 33 years revealed that the strong decline in cod biomass coincided with an increase in sprat biomass, a decrease in zooplankton density and an increase in phytoplankton density (Casini et al. 2008). The variations of sprat, zooplankton and phytoplankton biomass were mainly explained by the biomass of cod, while bottom-up processes and climate-hydrological factors had weaker influences. Clear negative relationships between adjacent trophic levels over time indicate the presence of a trophic cascade. The decline in cod biomass is strongly related to high fishing pressure. However, degradation of cod spawning grounds (lack of salt- and oxygen-rich bottom water) also made the cod stocks more sensitive to fishing (Österblom et al. 2007). Therefore, fishing and eutrophication had synergistic effects on cod stocks (Österblom et al. 2007, Casini et al. 2008). Sprat can (in contrast to herring) control zooplankton biomass in summer and thereby indirectly regulate the phytoplankton biomass. Therefore, sprat is suggested to play a key role for the mediation of both top-down (from fisheries) and bottom-up (from eutrophication) processes (Casini et al. 2008). Casini et al. suggest that the cyanobacteria-dominated summer bloom in the Baltic is top-down controlled and may be enhanced by eutrophication, in contrast to the spring bloom which is dependent on the winter nutrient level (Casini et al. 2008).
The major part of commercial fisheries takes place in open waters, but also coastal fishery is conducted along the Baltic coastline, targeting marine species such as herring, *Salmo salar* L (Atlantic salmon), *Salmo trutta trutta* L (Sea trout), *Platichthys flesus* (L) (European flounder) and cod, as well as freshwater and migratory species such as *Esox lucius* L (Northern pike), *Sander lucioperca* (L) (Pike-perch) and *Perca fluviatilis* L (European perch) (ICES 2009). The fishing activity has, similar to the open water, large effects on the fish community composition. For example, increasing coastal fishing in Estonia in the 1990s led to a strong decline in catch-per-unit-effort of perch (CPUE) (HELCOM

2006). Declines in perch and pike stocks have also been reported from coastal areas in the western Baltic Proper (Figure 1.5), which were due to recruitment failures (Ljunggren et al. 2010). Simultaneous to the declines in many large coastal fish species, the small-bodied three-spined stickleback *Gasterosteus aculeatus aculeatus* L largely increased in numbers (HELCOM 2006).

Similarly to the open water system, eutrophication affects the fish composition. Specifically cyprinids (e.g. *Rutilus rutilus* (L) (roach)) are suggested to benefit from eutrophication, because monitoring of the coastal areas showed that all except one area (Kvädöfjärden) were developing towards a more cyprinid-dominated state (HELCOM 2006).

Thus, fishing in both open Baltic Sea and coastal areas, as well as eutrophication, affect both open and coastal systems. However, cross-ecosystem effects also occur e.g. via food webs. Lower zooplankton biomass in open waters (caused by strong decline in cod) led to reduced zooplankton biomass in coastal waters, thereby causing a recruitment failure of pike and perch whose larvae largely depend on zooplankton food (Ljunggren et al. 2010).

In conclusion, the nutrient status of an ecosystem can affect its fish composition; and the fish composition can *vice versa* change the effects of eutrophication. Thus, a central part of this thesis is to test (i) if changes in higher trophic levels of coastal fish induce a trophic cascade similar to the demonstrated cascade in the open Baltic Sea, and (ii) if the changes in fish community composition interact with nutrient enrichment.

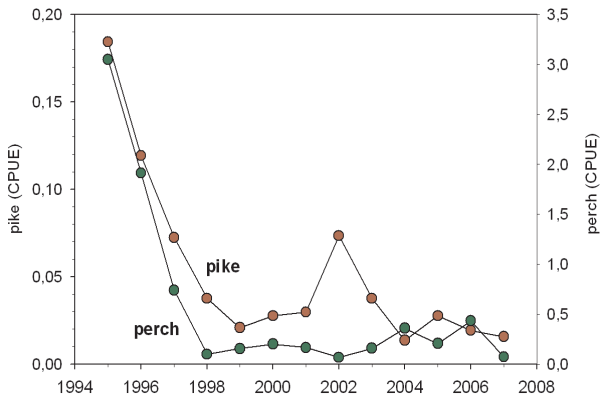



**Figure 1.5** Monitoring data of adult *Esox lucius* (pike, red, left y-axis) and *Perca fluviatilis* (perch, green, right y-axis) in catch-per-unit-effort (CPUE) from the area of Mönsterås. Modified after Ljunggren et al. 2010.

## 3. STUDY AREA AND SPECIES

The experimental studies included in this thesis were conducted in two different areas in the Swedish coastline of the Baltic Proper.

The **Askö study area** (N58°48' E17°40') (Figure 1.6) is located at the southern region of the Stockholm archipelago, and is a relatively open archipelago with good water exchange and a small catchment area dominated by forests (Kautsky 2008). The study site where the field experiments were conducted (Figure 1.7A) is shallow (about 1 m deep) and characterised by hard bottom with sandy patches in between. The mesocosm experiment was performed at the Askö field station (Figure 1.8).

The bladderwrack *Fucus vesiculosus* is a main habitat former in this rocky substrate and hosts a rich fauna, but also many algal species live epiphytically on the *Fucus*. Especially during summer, *Fucus* can be heavily overgrown by species of filamentous green and brown algae (Kautsky and Kautsky 2000), which can impair the *Fucus* growth and photosynthesis. The filamentous brown alga *Pylaiella littoralis* (L) Kjellman was the dominating epiphyte, but also diatoms (*Melosira* spp.) were found frequently on *Fucus*. Invertebrates and small fish use the *Fucus* as habitat and/or for foraging (Figure 1.7B), but some of them only pass their larval stages in the *Fucus* belt (Kautsky and Kautsky 2000). For example, many insect species spend a part of their life-history under water as larva and pupa and serve as an important diet for some fishes (e.g. Chironomidae). Likewise, the bivalves *Cerastoderma* spp. live as juveniles attached to the *Fucus*, whereas older individuals live burrowed in the sediment. The most frequently found grazing invertebrates belong to the groups of Amphipoda, Isopoda and Gastropoda (Table 1.1) and are grazing on epiphytes or the *Fucus* itself. Other invertebrates live attached to the *Fucus* but filter particles from the water column such as the barnacle *Amphibalanus improvisus* (Darwin), the blue mussel *Mytilus edulis* L, the bryozoan *Electra pilosa* (L) or hydroids. Further inhabitants of the *Fucus* belt are Mysida and decapod shrimps *Palaemon* spp., which are both highly mobile. The invertebrate fauna embraces a total of 37 species most of which belong to the taxonomic groups Insecta, Crustacea and Gastropoda (Figure 1.10, Table 1.1). Specifically, Chironomidae (59.1%), juvenile *Cerastoderma* spp. (19.2%) and small Gastropoda (11.3%) occurred in large numbers, whereas large individuals of *Theodoxus fluviatilis* (L) (48.4%), *Gammarus* species (12.2%) but also Chironomidae (11%) dominated the invertebrate biomass (Figure 1.10).

The fish fauna in the study area constitutes of small meso-predators to large top-predators from both marine and freshwater origins. Frequently found demersal fish species are gobies (*Gobius niger* L, *Pomatoschistus microps* (Krøyer) and *Pomatoschistus minutus* (Pallas)) as well as flounders. The most common pelagic species are *Phoxinus phoxinus* (L) (Eurasian minnow), three-spined stickleback, roach and *Pungitius pungitius* (L) (ninespine stickleback), which forage in schools in the *Fucus* belt. Furthermore, *Syngnathus typhle* L (broadnosed pipefish) are often found entangled in *Fucus*. Larger predators usually visit the *Fucus* belt when hunting for smaller fish. Common predatory fish are the freshwater species pike, perch and pike-perch.

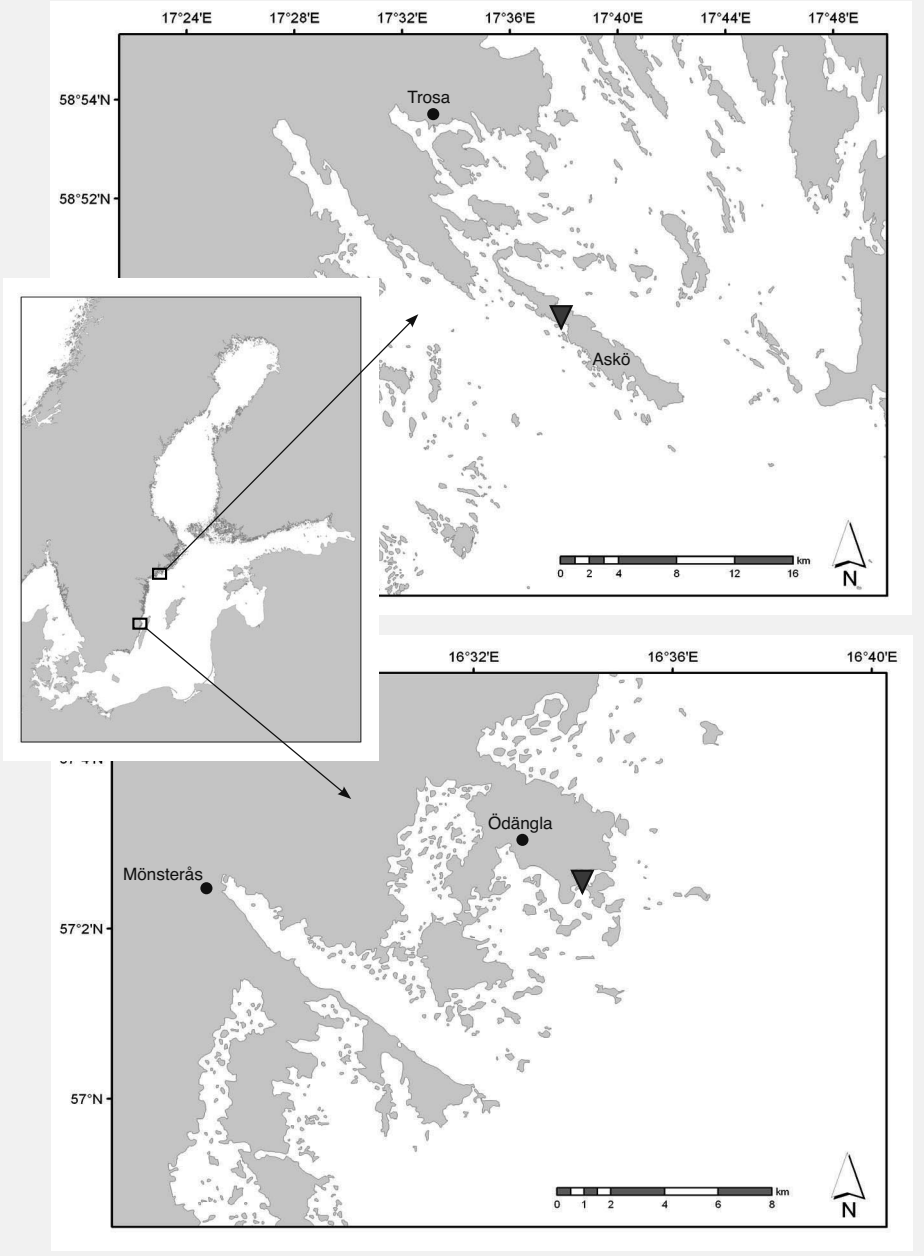



**Figure 1.6** Study areas at Askö (top) and Mönsterås (bottom). Experimental sites are indicated.

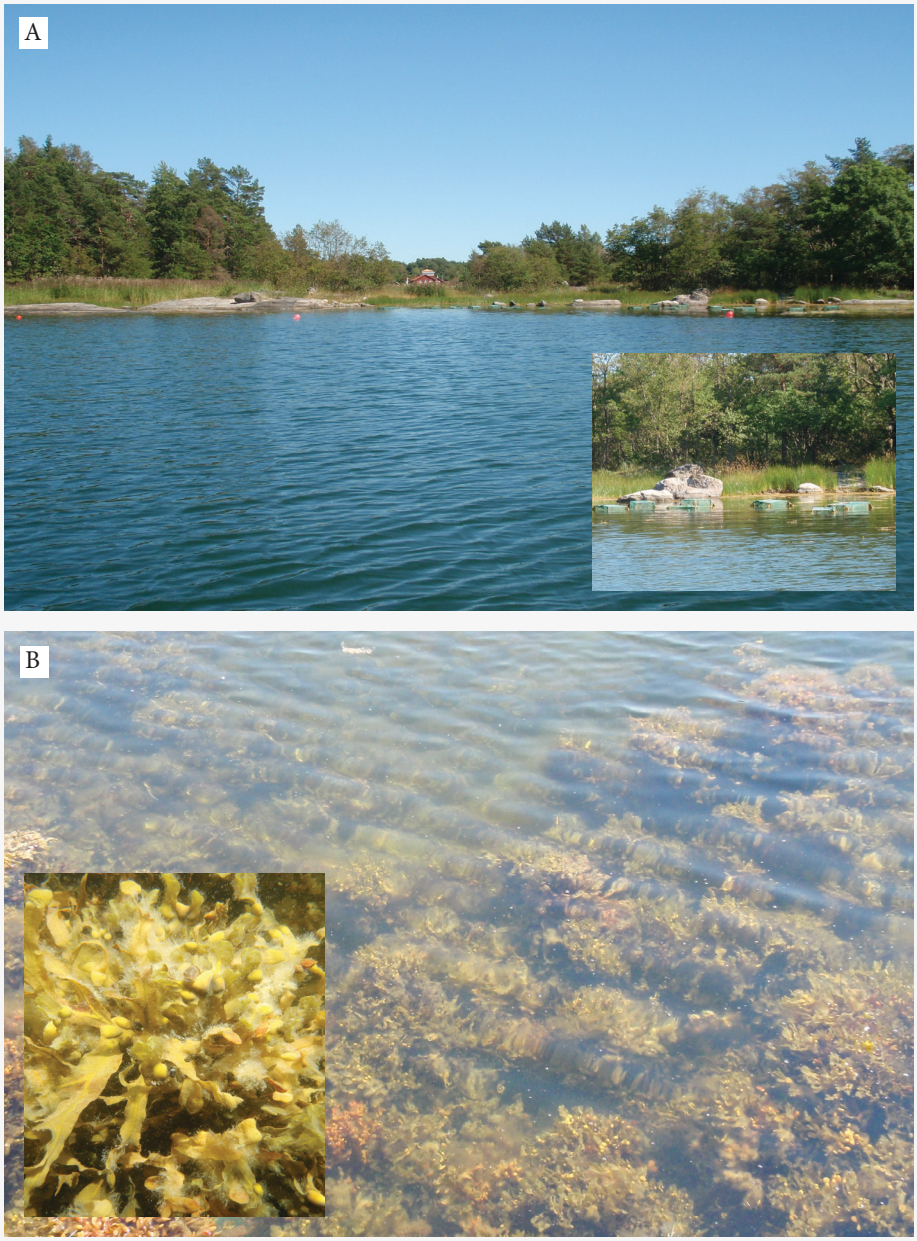



**Figure 1.7** The study site at Askö with the experimental cages in 2008 (A). *Fucus vesiculosus* is the dominant habitat-former at the study site (B) for a diverse invertebrate and epiphyte community (small photo).


**Figure 1.8** Setup of the outdoor mesocosm experiment. Buckets were arranged in a blocked design and supplied with filtered sea water from outside the harbour. After four weeks of the experiments an increased growth of microalgae was visible in the buckets including only gastropods (A), in contrast to buckets with only amphipods (B) (and no meso-predators).

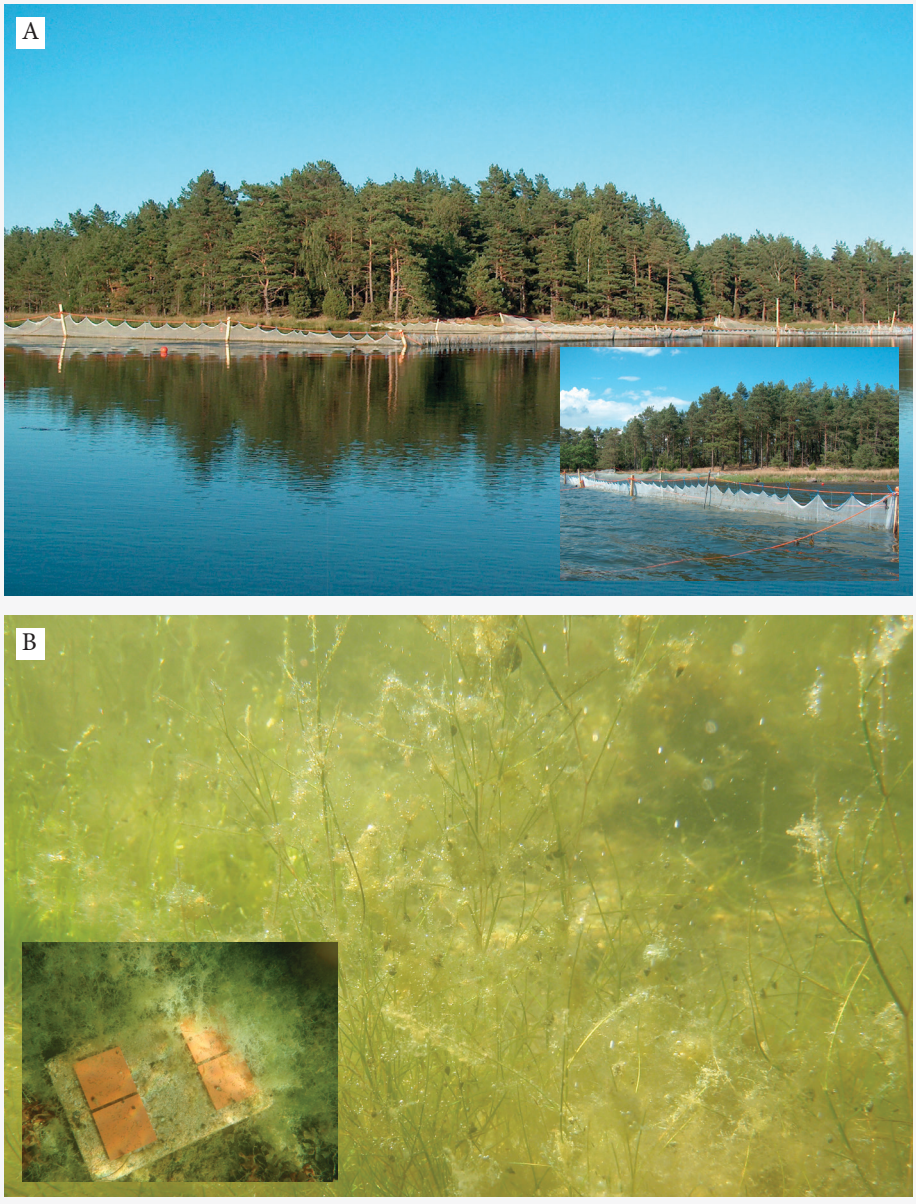



**Figure 1.9** The study site at Mönsterås with the large enclosure in 2008 (A). *Fucus vesiculosus* as well as the plants *Myriophyllum spicatum* and *Stuckenia* (= *Potamogeton*) *pectinata* (B) dominate the shallow sublitoral and provide habitat for the invertebrate and epiphyte communities. Bricks with tiles glued on the top (small photo) were placed to measure algal growth.

The **Mönsterås area** (Ödängla, Mönsterås, N57°3' E16°33') is a sheltered and shallow area in the Kalmar strait, between the province of Småland and the island Öland (Figure 1.6). The sediment is mainly soft bottom and scattered with boulders. The vegetation is, in contrast to the Askö area, more diverse. *Fucus* is only in the upper sub-littoral the dominant habitat former. In deeper waters, the submerged vegetation consists mainly of the Eurasian water milfoil *Myriophyllum spicatum* L and the pondweed *Stuckenia pectinata* (formerly *Potamogeton pectinatus*) (L) Börner (Figure 1.9). The two plant species host invertebrates as well as epiphytes (mainly filamentous green algae) similar to *Fucus*. The invertebrate community differs only slightly from the communities at Askö. We found a total of 44 species, mainly from the taxonomic groups Insecta, Gastropoda and Amphipoda. The total biomass was strongly dominated by the freshwater gastropod species *Bithynia tentaculata* (L) (34.8%), *Theodoxus fluviatilis* (20.7%), *Potamopyrgus antipodarum* (JE Gray) and *Radix* spp. (10.3% each). The only marine gastropods *Hydrobia* spp. added 12.5% to the total biomass. The invertebrate abundance was dominated by *Hydrobia* spp. (24.5%) and larvae of Chironomidae (23.7%).
Three-spined stickleback is the dominant fish species in summer. Other common fishes are the pelagic freshwater species *Alburnus alburnus* (L) (bleak), *Scardinius erythrophthalmus* (L) (rudd), *Blicca bjoerkna* (L) (white bream) and roach. Perch and pike represent the larger predators.

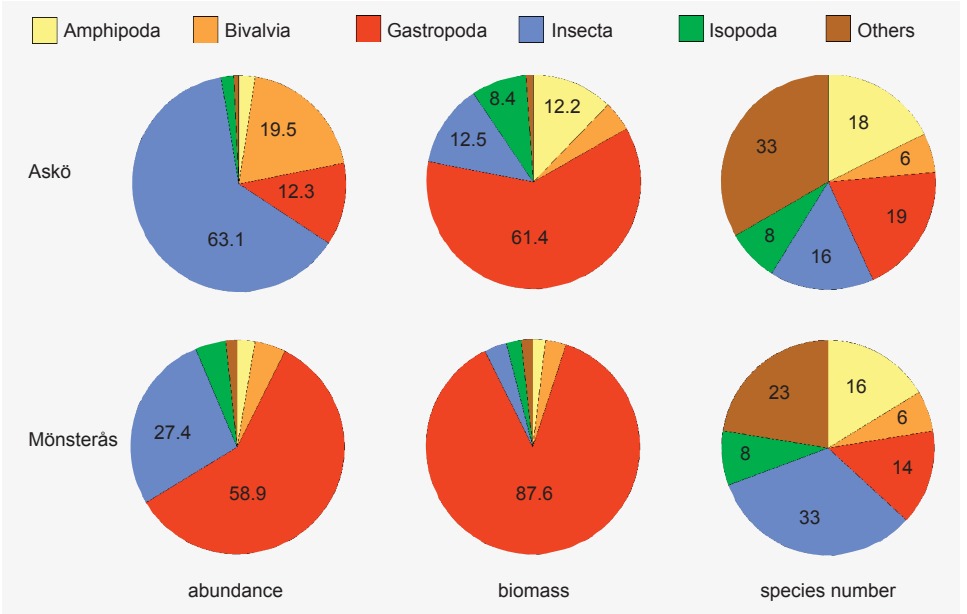



**Figure 1.10** Invertebrate composition at the study sites Askö and Mönsterås. Shown are relative abundance (left), relative biomass (middle), and relative species number (right) of the major taxonomic groups. Biomass ratios are calculated from ash-free-dry weights.

**Table 1.1** Invertebrate species from both study areas that live associated with *Fucus vesiculosus* with their major feeding mode: **C** – collector, **FF** – filter feeder, **G** – grazer, **SF** – suspension feeder, **DF** – deposit feeder, **P** – predator, **O** – omnivore, **U** – undetermined
Determination of feeding modes are based on: Kofoed 1975, Berglund 1980, Hayward & Ryland 1990, MacNeil et al. 1997, Goecker & Kåll 2003, Orav-Kotta & Kotta 2003, Zettler et al. 2004, Janas & Barańska 2008, Barz & Hirche 2009, www.waterbugkey.vcsu.edu

| | | | |
|---|---|---|---|
| **Acari** | P | **Harpacticoida** | O |
| **Amphipoda** | | **Hirudinea** | P |
| *Corophium volutator* (Pallas) | G, DF | | |
| *Corophium* spp. | G, DF | **Hydrozoa** | SF |
| *Gammarus locusta* (L) | | | |
| *Gammarus oceanicus* Segerstråle | | **Insecta** (as larvae) | |
| *Gammarus salinus* Spooner | G | Ceratopogonidae | P |
| *Gammarus zaddachi* Sexton | (P) | Chironomidae | C/P |
| *Gammarus inaequicauda* Stock | | Coenagrionidae | P |
| *Gammarus* spp. | | Corixidae | P/O |
| *Leptocheirus pilosus* Zaddach | G | Dytiscidae | P |
| | | Ephydridae | C |
| **Bivalvia** | | Haliplidae | O |
| *Cerastoderma* spp. | FF | Hydroptilidae | U |
| *Macoma balthica* (L) | FF | Hydrophilidae | P |
| *Mytilus edulis* L | FF | Libellulidae | P |
| | | Limnephilidae | G (P) |
| **Bryozoa** | | Phryganeidae | O |
| *Einhornia* (= *Electra*) *crustulenta* (Pallas) | SF | Polycentropodidae | C (P) |
| *Electra pilosa* (L) | SF | **Isopoda** | |
| | | *Asellus aquaticus* (L) | G |
| **Cirripedia** | | *Idotea balthica* (Pallas) | G (P,O) |
| *Amphibalanus improvisus* (Darwin) | SF | *Idotea chelipes* (Pallas) | G |
| | | *Idotea* spp. | G |
| **Decapoda** | | *Jaera* (*Jaera*) *albifrons* Leach | G |
| *Palaemon adspersus* Rathke | O | | |
| *Palaemon elegans* Rathke | O | **Mysida** | |
| *Palaemon serratus* (Pennant) | O | *Neomysis integer* (Leach) | O |
| | | *Praunus flexuosus* (Müller) | O |
| **Gastropoda** | | *Praunus inermis* (Rathke) | O |
| *Bithynia tentaculata* (L) | G | | |
| *Peringia* (= *Hydrobia*) *ulvae* (Pennant) | G, DF | **Nemertea** | P |
| *Ventrosia* (= *H.*) *ventrosa* (Montagu) | G, DF | **Oligochaeta** | |
| *Hydrobia* spp. | G, DF | Naidinae | O |
| *Lymnaea stagnalis* (L) | G | | |
| *Potamopyrgus antipodarum* (JE Gray) | G | **Ostracoda** | FF |
| *Radix balthica* (L) | G | **Polychaeta** | |
| *Radix labiata* (Rossmassler) | G | *Nereis* spp. | P |
| *Stagnicola palustris* (OF Muller) | G | | |
| *Theodoxus fluviatilis* (L) | G | | |
| *Tenellia adspersa* (Nordmann) | P | | |

## 4. THESIS OUTLINE



The aim of this thesis is to examine the effects of fish composition and nutrient availability on the food web. Specifically, I test combined effects of nutrient enrichment and top-predator removal (Chapter 2), fish diversity (Chapter 3), and a large-scale mesopredator release (Chapter 5), respectively. In a further experiment, I investigate the specific role of omnivores on herbivore and algal assemblages (Chapter 4). Finally, monitoring data are compiled to show the interactive effects of offshore and coastal food webs (Chapter 6). In Chapter 7, I summarise the main findings.

All experiments were based on the same food web (Box 1.5) but focus on different aspects and were applied on different spatial scales. In experimental ecology, the choice of the spatial scale has important implications for the feasibility and practicability of the experiment as well as the applicability of the resulting data. Field experiments on a large scale deliver the most natural results and have therefore the highest applicability value for predictions or ecosystem management issues. However, the practicability and control over the experiment declines with increasing size of the experimental plots. In contrast, mesocosm experiments allow a higher repetition and are less influenced by natural variation, but the extrapolation of their results to natural systems is limited. This thesis combines different approaches (mesocosm, small-scale field experiments and large-scale field experiment) in order to gain a more comprehensive understanding of the species interactions in a food web context.

The Baltic Sea was chosen as study system because of its low species diversity that also simplifies the food web architecture. The study food web embraced fishes, invertebrates and algae interlinked as displayed in Box 1.5. From the diverse benthic invertebrates (see also Plate 1.1 and Table 1.1) only the species that feed on benthic algae were included.
The chapters in this thesis are structured around the following aspects:

In **Chapter 1**, I introduce food webs as networks that combine all organisms in an ecosystem. I described some internal factors (such as omnivory, diversity) that can regulate the food web configuration. I also give some examples of human-driven external factors (such as fishing and nutrient input) and their effects on food webs.

In **Chapter 2**, I test effects of declining larger predatory fish on a coastal food web in the Baltic Sea. In a small-scale predator exclusion experiment, we analysed the changes in food web configuration when top-predators were present or absent. We determined the resulting density of the next lower trophic level (meso-predatory fish) as well as both abundance and biomass of the following two trophic levels (herbivores and algae). We demonstrate that **the removal of top-predators combined with nutrient enrichment propagates through the food web to increase algal growth**.

In **Chapter 3**, I test the effects of multiple predator species with varying densities on herbivore and algal assemblages. In a field experiment, cages were enclosed with different sets of predators (three species in monocultures and a mixture) at different predator densities and we recorded abundance and biomass of herbivores as well as algae. We show

that **predator identity had strong effects on the herbivore assemblages in fish monocultures, which were attenuated in the mixed assemblages. However, trophic cascading effects on producers were more dependent on predator density and nutrient enrichment.**

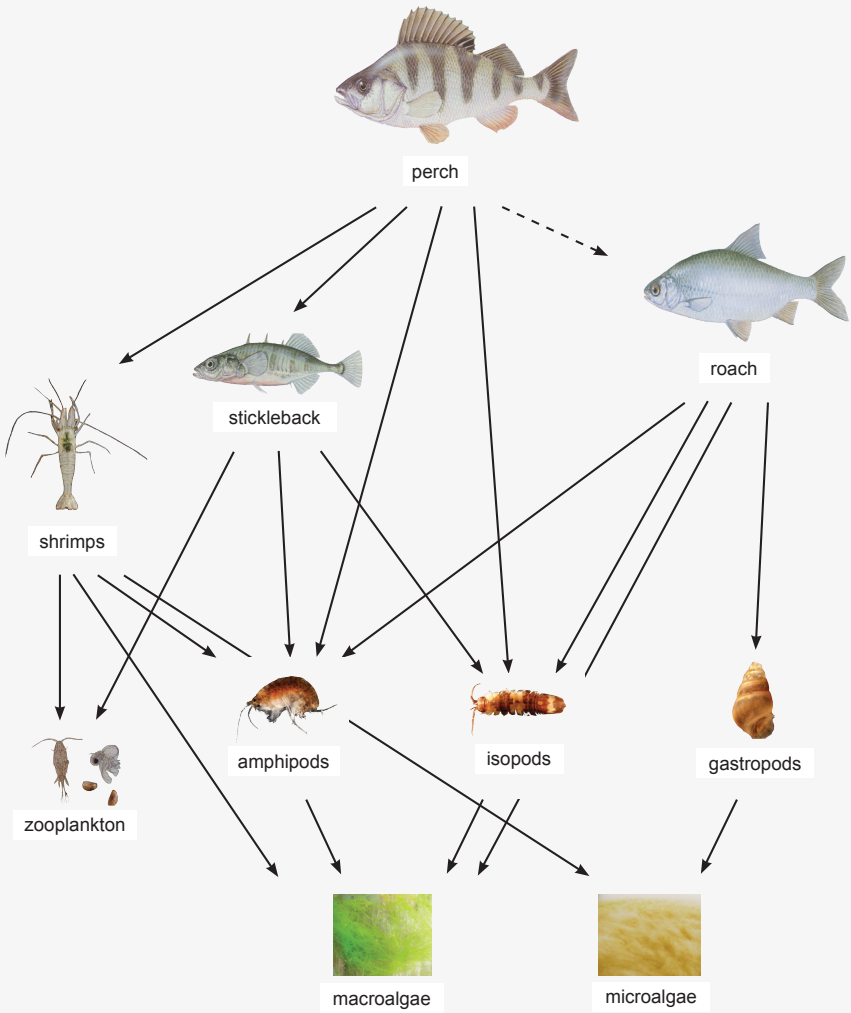
In **Chapter 4**, we test the effects of omnivory in trophic cascades. In a mesocosm experiment, we assembled herbivore communities with representatives of the two main functional groups (amphipods and gastropods). Half of the mesocosms contained an omnivorous shrimp (meso-predator) and half did not, and the resulting production of micro- and macroalgae was recorded. We show that **omnivory can dampen enhanced top-down effects from a meso-predator release**.

In **Chapter 5**, I test effects of a large-scale meso-predator release on the coastal food web structure. This study was performed in an area where top-predator abundance declines while the density of meso-predators strongly increases. In large enclosures (20 x 30 m), meso-predators were in- or excluded, and trophic effects on herbivores and algae were measured. With this large-scale approach, we test effects of a meso-predator release on an ecosystem-scale that could be relevant for ecosystem management. We show that **a meso-predator release increase macroalgal recruitment through compositional changes of the herbivores.**

In **Chapter 6**, we combine offshore-and coastal monitoring data to test for effects of offshore fisheries on coastal food webs. We demonstrate that **offshore- and coastal food webs interactively affect one another.** This has substantial implications for management because it emphasises the need for an ecosystem-wide management (e.g. of fisheries or nutrient input) but also the need for cross-ecosystem management.

In **Chapter 7**, I summarise the key findings and present hypothetical scenarios of synergistic effects of top-down and bottom-up forces. I hypothesise that the functional trait composition of the herbivore community determines the propagation of top-down effects (to producers) and bottom-up effects (to predators).

## Box 1.5 Simplified trophic interactions of the studied organsisms




Food web interactions of species groups included in this thesis. *Perca fluviatilis* (perch) constitutes the top-predator. The omnivorous *Rutilus rutilus* (roach), *Gasterosteus aculeatus aculeatus* (three-spined stickleback) and the omnivorous *Palaemon* spp. (shrimp) are meso-predators. Perch predates on juvenile roach and perch but on all sizes of stickleback. Amphipods (*Gammarus* spp.), isopods (*Idotea* spp. and *Jaera (Jaera) albifrons*) and gastropods (including *Hydrobia* spp. and *Theodoxus fluviatilis*) represent the dominating grazer groups associated with *Fucus*. Macroalgae refer here to ephemeral filamentous algae, while microalgae are unicellular algae which may form colonies, such as diatoms and cyanobacteria. Arrows indicates direction of predation.
Fish drawings are from Gerstmeier and Romig 1998.

2

# Cascading effects from predator removal depend on resource availability in a benthic food web

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Anneke K. Rippen
Britas Klemens Eriksson

*Marine Biology* 158: 391-400

## Abstract

We tested joint effects of predator loss and increased resource availability on the grazers' trophic level and the propagation of trophic interactions in a benthic food web by excluding larger predatory fish from cages and manipulating nutrients in the coastal zone of the Baltic Sea. The combination of nutrient enrichment and excluding larger predators induced an increase in medium-sized predatory fish (three-spined stickleback). The meso-predator fish in turn did not change the total abundance of the invertebrate herbivores, but did cause a substantial shift in their community composition towards the dominance of gastropods by reducing amphipods by 40–60%, while gastropods were left unchanged. The shift in grazer composition generated a 23 times higher producer biomass, but only under nutrient enrichment. Our results show that top-predator declines can substantially shift the species composition at the grazers' level, but that cascading effects on producers by a trophic cascade strongly depend on resource availability.

## Introduction

World-wide declines in top-predator communities have altered the structure and dynamics of food webs across ecosystems (Myers and Worm 2003, Sala 2006, Heithaus et al. 2008). Declines in large predators may generate community-wide trophic cascades as it was shown for example for lakes (Carpenter et al. 1985) and benthic marine systems (Estes et al. 1998), where increases of medium-sized predators (meso-predator release) induce reciprocal changes in the total abundance of adjacent trophic levels (Pace et al. 1999). However, such examples are limited because most natural ecosystems are not simple food chains with homogenous trophic levels, but rather highly interactive food webs where different trophic levels are composed of species with different functional traits (Steiner 2001, Vasas et al. 2007). Thus, we would predict that changes in predator abundances should affect the species composition instead of the total abundance of prey (Duffy 2002) and that predator identity should determine which prey groups increase or decrease. This predator heterogeneity becomes particularly apparent at higher trophic levels where omnivory and intraguild predation are common, which may dilute effects of single species groups in the food web and weaken trophic cascades (Polis and Holt 1992, Stachowicz et al. 2007).



Trophic cascades are enhanced by ecosystem productivity (Oksanen et al. 1981, Pace et al. 1999), which would suggest that effects of top-predator declines closely interact with another global trend, eutrophication. The effects of nutrient enrichment in food webs in turn depend on the strength of top-down control (Gruner et al. 2008). In systems with strong top-down control we expect nutrient enrichment mainly to increase the abundance of prey species that are resistant to predation. Gruner et al. (2008) referred to this scenario as 'induced resistance'. In systems with weak top-down control, we mainly expect fast-growing prey species to increase from nutrient enrichment ('tolerance'). Nutrient effects on producer biomass then depend on different grazer species abilities to utilise and incorporate the increased quantity and quality of their food resource (Hillebrand and Kahlert 2001).

In this study we tested joint effects of removing larger fish and nutrient enrichment on a coastal food web in the Baltic Sea. In the Baltic Sea, local declines of the dominant larger predatory fish *Perca fluviatilis* L (European perch) and *Esox lucius* L (Northern pike) coincide with soaring abundances of smaller bodied fish, mainly *Gasterosteus aculeatus aculeatus* L (three-spined stickleback), and a resulting enhancement of filamentous algae (Eriksson et al. 2009). In earlier experiments we demonstrated that this is caused by a trophic cascade where a meso-predator release of stickleback increased the growth of filamentous algae by decreasing grazing rates. However, grazer responses to predator exclusion were ambiguous, and no changes in the abundance of grazers that are effective consumers of macroalgae (e.g. amphipods and isopods) were found. Instead, we only detected compositional changes in the invertebrate community that depended on higher bivalve abundances and lower abundances of small gastropods (< 2 mm), of which only the small gastropods could constitute a link between the exclusion of large predators and the enhanced algal biomass production. In this study we therefore focus on the response of the grazer composition to top-down and bottom-up forces with respect to

different grazer functional groups, to specifically understand which responses of the grazer community contribute to the documented changes in grazing rates.

At present, perch (carnivore) and stickleback (facultative planktivore) are among the most abundant coastal fishes in the Baltic Sea (Ådjers et al. 2006). Herbivores are dominated by crustacean grazers (amphipods and isopods), which are consumed by both perch and stickleback and gastropods, which only play a minor role in the diet of perch and are not eaten by stickleback (Lappalainen et al. 2001). Moreover, the grazers have distinctly different feeding strategies: amphipods and isopods are efficient macroalgal grazers while gastropods mainly consume microalgal film (Råberg and Kautsky 2007b). We tested the hypothesis that trophic cascades from declines in top-predators to primary producers depend on both the functional traits of their prey and resource availability, by field manipulations of the coastal fish community and nutrients. Specifically, we hypothesise that removing larger predatory fish generates a meso-predator release of stickleback, that together with nutrient enrichment cascade down the food web to increase the biomass of filamentous macroalgae, by changing the composition of the grazer community towards stronger dominance of gastropods (which are unpalatable to sticklebacks and inefficient grazers on macroalgae).



## Methods

### Study system and organisms

The brackish water of the western Baltic Sea is non-tidal and characterised by low species diversity. The coastal fish community consists of both marine and freshwater species. *Perca fluviatilis* (hereafter perch) and *Gasterosteus aculeatus aculeatus* (hereafter stickleback) are among the most abundant fish species in the study area (Eriksson et al. 2009). Perch as a top-predator is strictly carnivorous and undergoes three major dietary shifts during its ontogeny, first feeding on zooplankton, then on macroinvertebrates and finally on fish (Lappalainen et al. 2001, Kahl and Radke 2006 and references therein). Large perch is therefore mostly piscivorous and feeds on juvenile stages of roach and perch (Eklöv and Persson 1995) and stickleback (pers. obs.), but also on crustaceans (Lappalainen et al. 2001). Stickleback is an important meso-predator in the system, which prefers zooplankton over benthic prey. However, as the availability of zooplankton decreases zoobenthos becomes more important (Ibrahim and Huntingford 1989). Stickleback mainly feeds on copepods, gammarid amphipods and larvae of Chironomidae (pers. obs.) in the study area.

The experiment was performed in subtidal communities, dominated at the basal level by the seaweed *Fucus vesiculosus* L (hereafter *Fucus*), which provides important habitat for associated filamentous macroalgae (e.g. *Cladophora glomerata* (L) Kützing, *Pylaiella littoralis* (L) Kjellman and *Ulva* spp.) and an invertebrate grazer assemblage dominated by amphipods (mainly *Gammarus* spp., hereafter *Gammarus*), gastropods (mainly *Theodoxus fluviatilis* L and *Hydrobia* spp., hereafter *Theodoxus* and *Hydrobia*) and isopods (mainly *Idotea* spp. and *Jaera albifrons* (Leach), hereafter *Idotea* and *Jaera*) (Råberg and Kautsky

2007a, Wikström and Kautsky 2007). *Theodoxus* and *Hydrobia* are efficient consumers of diatoms and microalgae (Kofoed 1975, Råberg and Kautsky 2007b). *Gammarus* species are considered selective omnivores, feeding on filamentous macroalgae and larger plant material, as well as fine detritus, other invertebrates and fish eggs (MacNeil et al. 1997, Orav-Kotta and Kotta 2003). Thus, the grazer community is dominated by species of two different feeding groups: (1) 'shredders' (amphipods and isopods) that consume macroalgae and are potential prey for both perch and stickleback, and (2) 'scrapers' (gastropods) that mainly consume benthic microalgae, and that are probably unpalatable to stickleback and only of minor importance to perch. Therefore, we only included amphipods, isopods, and gastropods from the total invertebrate assemblages into our analyses.



## Field experiment

The field experiment was conducted at the Askö Laboratory, western Baltic Sea, Sweden (58°48'N, 17°40'E). We tested the hypothesis of joint effects of large predatory fish and nutrient enrichment on the grazer and macroalgal community by excluding larger fish and adding agricultural fertiliser.

The experiment was designed as a factorial combination of large predatory fish (open/closed cages) and nutrient enrichment (ambient/enriched) with 5 replicates per treatment (= 20 plots). The experiment ran for 12 weeks from 22 June to 17 September 2007. We placed steel-framed cages (120 × 55 × 100 cm, length × width × height), covered with a plastic net (mesh size 1.4 cm), in shallow water (1 m deep). Partial cages (= 'open') were used to separate cage from predation effects (Steele 1996) and had openings (diagonally half-opened per side) on two non-opposite sides where larger fish could enter (see Figures and Tables in Appendix). The closed cages could only be accessed by small fish (size of sticklebacks) through the mesh. Stickleback access to the cages was examined during snorkelling observations every one to two weeks during the experiment. Perch was frequently observed in the study area but could not be counted per cage, because they disappeared too quickly when disturbed by the snorkelling observations. Coated slow-release N-P-K fertiliser pellets (Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany) were used to continuously enrich the water column with nitrogen (14%, as $NH_4$-N and $NH_3$-N), phosphorus (9%, as $P_2O_5$) and potassium (15%, as $K_2O$). The fertiliser was supplied from elongated mesh bags (20 × 10 cm, 1 mm mesh size, 120 g per bag, 4 bags per enriched cage) that were placed in two opposite corners and two opposite long sides of the enriched cages. Fertiliser bags were replaced after 6 weeks. This method has already been validated to enrich the water column (Worm et al. 2000) and to subsequently increase producer biomass (Hillebrand and Kahlert 2001). The enrichment resulted in 49–69% higher levels of total phosphorus (as $PO_4^{3-}$) and 105–187% higher levels of total nitrogen (as $NH_4^+$,$NO_3^-$/ $NO_2^-$), inside the enriched cages in June and July respectively (ambient nutrient levels: June: total P = 4.17 ± 0.1346 µg $L^{-1}$, total N = 5.12 ± 1.0846 µg $L^{-1}$; July: total P = 2.95 ± 0.2046 µg $L^{-1}$, total N = 3.64 ± 0.46 µg $L^{-1}$; mean ± SE; see Figures and Tables in Appendix for statistics). The increase in nutrient

concentrations in the enriched plots relative to the ambient levels was half the magnitude of the measured differences between a regularly monitored eutrophied site 20 km to the north and the oligotrophic study site in summers between 1990 and 2000 (Granéli et al. 1990). Cages were placed at least 3 m apart from each other to avoid cross-fertilisation and followed a randomized block design. Periphyton was brushed off from the outside of the cages once per week.

Invertebrate communities were collected by using *Fucus* as a sampling unit. Therefore, bundles of *Fucus* with no visible epiphytes were collected near the study area prior to the start of the experiment, cleaned from epifauna and anchored to a brick. One bundle of *Fucus* (41.7 ± 1.4 g DW, mean ± SE, n = 30) was placed inside each cage. In order to control for cage artefacts a no-cage-plot was included by placing one *Fucus* outside of each open cage for pair-wises comparisons with the according open cages. Invertebrates were sampled by pulling a net bag (mesh size 1 mm) over each *Fucus* bundle, enclosing all of the associated fauna under water. Invertebrates were sampled twice, on 5 July and at the end of the experiment on 17 September. Only the first sample was used in the analyses, as the meso-predator stickleback moved away from the coastal zone in late July (see results), making the predator treatment of little relevance for the mobile invertebrates in September. Animals were sorted under a dissecting microscope, determined to species level if possible, counted and dried at 60 °C for at least 48 h to determine dry weight. Dry weight was converted to ash-free dry weight by using species-specific conversion factors (Lappalainen and Kangas 1975). All invertebrate data were recalculated to abundance and biomass per 100 g DW of *Fucus*.

Net production of macroalgae was examined with the use of unglazed ceramic tiles (5 cm × 5 cm) as a substrate, which were glued on bricks (4 tiles on each brick). One brick was placed in each cage. In previous studies the applicability of these tiles as settling substrate for macroalgae has been proven successfully (Worm and Lotze 2006, Eriksson et al. 2009). Macroalgae were sampled at the end of the experiment, sorted under a dissecting microscope, determined to species level if possible and dried at 80 °C for at least 48 h to determine dry weight.

## Statistical analyses

Grazer data was highly skewed and variances strongly heterogeneous also after strong transformations. We therefore analysed all data with Generalized Linear Mixed Models (GLMM). We used untransformed data in models with normally distributed error structures and log-link functions, after comparing models with different link functions for the best fit (log-likelihood). As explanatory variables, the model included the fixed main factors "predator" (closed vs. open) and "nutrients" (ambient vs. enriched), as well as the interaction between the predator and nutrient treatments and the random factor "block". The block factor represents the spatial distribution of the cages in the field. Fisher's LSD post-hoc-tests were applied when significant interaction effects were found. *Fucus* bundles outside of each open cage (N = 10) were used to test for cage effects on grazers. Paired t-tests were adopted to pairwise compare grazers outside and inside of the open cages. No

significant differences between the open cages and outside were found for amphipods, isopods and gastropods (see Appendix for the statistics). Macroalgal biomass data was distributed bimodally with half of the values close to zero (ambient cages) and the other half 10–20 times higher (enriched cages). We therefore split the dataset and analysed ambient and enriched treatments separately applying GLMM as above. Stickleback densities were analysed following the same procedure as for the grazers.

In order to control for Type I error rates from the multiple testing in our data set, we Bonferroni corrected the significance levels to $\alpha = 0.0167$ for grazer data and $\alpha = 0.025$ for algal data. Quantity was tested three times in each grazer group (biomass, abundance and mean individual size) and twice for macroalgae (one in ambient and one in enriched conditions).



## Results

Overall, our results show that excluding larger predatory fish and adding nutrients together increased the abundance of meso-predator fish and simultaneously the biomass of filamentous macroalgae. Therefore, a trophic cascade from excluding larger predatory fish was only induced under elevated nutrient levels, through a meso-predator release and the reduction of palatable grazers (amphipods), which resulted in increased algal biomass.

The meso-predator stickleback strongly dominated the smaller bodied fish fauna. Stickleback abundances increased in the closed cages, but only when they were nutrient enriched (Figure 2.1a; GLMM: interaction effect, $\chi^2 = 7.25$, $P = 0.007$). During four

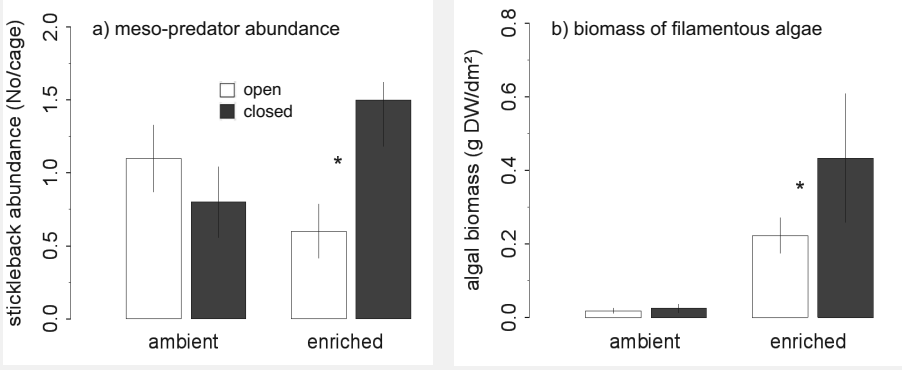


**Figure 2.1** Experimental effects on **a)** stickleback (*Gasterosteus aculeatus*) abundance (means ± SE, N = 5), and **b)** total biomass of filamentous algae (means ± SE, N = 5) in cages open (white bars) and closed (grey bars) for large predatory fish under ambient and enriched nutrient levels. **a)** Stickleback numbers were significantly higher when excluding larger predatory fish under enriched conditions (GLMM: P = 0.007). * indicates a significant post-hoc result (P = 0.026). **b)** Macroalgal biomass was significantly higher when excluding large predatory fish under enriched conditions. * indicate significant predator effects in separate GLMMs for enriched cages only (ambient: P = 0.03, enriched: P < 0.003).

snorkel samplings in late June and early July we counted 1.5 ± 0.3 (mean ± SE, N = 5) stickleback inside the closed enriched cages, which was 2.5 times more than in the open enriched cages (post-hoc LSD-test, P = 0.026). After July, stickleback decreased strongly in abundance and vanished from the coastal zone (all counts in August were zero). Stickleback numbers in the ambient cages did not differ between the predator treatments.

The macroalgal community was dominated by three filamentous species: *Cladophora glomerata*, *Pilayella littoralis* and *Ulva* spp. Total macroalgal biomass was on average 15 times higher in the enriched cages (0.328 ± 0.093, mean ± SE, N = 10) than in the ambient cages (0.022 ± 0.007, mean ± SE, N = 10). In the enriched cages the exclusion of large predatory fish induced a doubling in algal biomass (Figure 2.1b; GLMM: $\chi^2$ = 9.04, P = 0.003). In the ambient cages there was overall very low macroalgal biomass and no significant effect of the predator treatment was found (GLMM: $\chi^2$ = 4.61, P = 0.031). Therefore, nutrient enrichment strongly increased algal biomass and predator exclusion generated together with nutrient enrichment a 23 times higher algal biomass (Figure 2.1b). Thus, only under elevated nutrient levels exclusion of larger predatory fish induced a meso-predator release that cascaded down the food web to increase the production of filamentous algae indicative of an algal bloom.

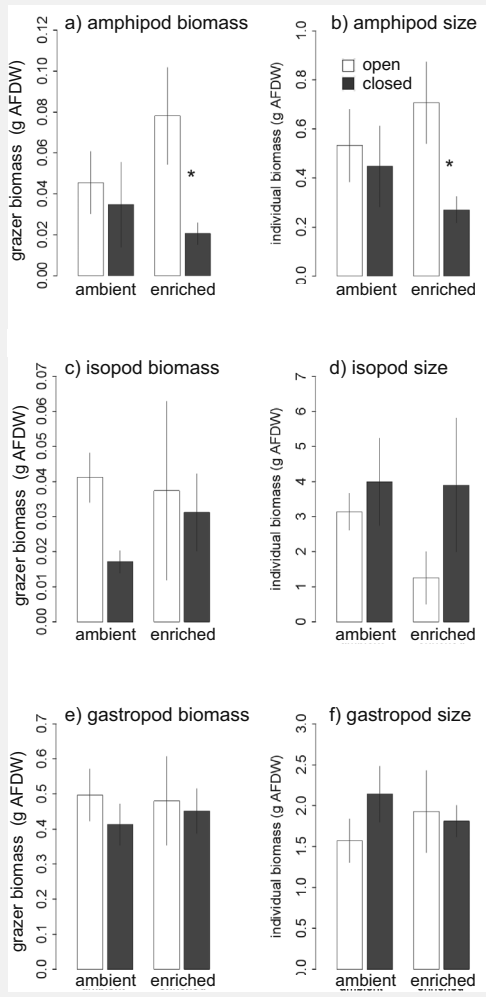


**Figure 2.2** Grazer biomass and individual biomass in cages open (white bars) and closed (grey bars) for large predatory fish under ambient and enriched nutrient levels. Biomass was calculated per 100 g Fucus DW (mean ± SE, N = 10). Predator treatment showed significant main effects from GLMM for amphipod biomass (P = 0.002) as well as for amphipod size (P = 0.0003). There was a significant interaction effect for amphipod size (P = 0.05) and a statistical trend for amphipod biomass (P = 0.031). * indicate significant post-hoc results for the predator treatment under elevated nutrient levels (P < 0.02). No significant differences between the treatments on biomass or size were found for isopods and gastropods.

Excluding larger predatory fish also affected the composition of invertebrate grazers. Mean amphipod biomass was reduced by more than half in the cages where large fish was excluded (Figure 2.2a; Table 2.1). There was no significant interaction between the predator and the nutrient treatment, but a trend towards significance (Table 2.1; P = 0.032). Post-hoc tests revealed that this trend was due to predator effects only in the enriched cages (post-hoc LSD-tests on predator treatment: ambient: P = 0.619, enriched: P = 0.019). This may suggest that predator exclusion decreased amphipod biomass mainly under elevated nutrient levels, whereas predator effects were absent under ambient levels. Amphipods were significantly smaller when predators were excluded, but only when nutrients were added (Figure 2.2b; Table 2.1; significant interaction effect, post-hoc LSD-tests on predator treatment: ambient: P = 0.581, enriched: P = 0.013). Total amphipod abundance was not affected. Excluding large predatory fish reduced isopod abundance by 46%, although differences were not statistically significant they showed a strong trend (Table 2.1; P = 0.019). Predator effects on isopods did not interact with the nutrient treatment. No effects on isopod biomass and mean individual weight were found (Figure 2.2c–d). Gastropod biomass, abundance and mean individual weight were not significantly affected by any of the experimental treatments (Figure 2.2e–f; Table 2.1).



**Table 2.1** Results from Generalized Linear Mixed Model on the predator exclosure and nutrient enrichment on grazer biomass, abundance and individual mean biomass (size).

| Source of variation | | Biomass | | Abundance | | Size | |
|---|---|---|---|---|---|---|---|
| | Df | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P |
| **Amphipods** | | | | | | | |
| Predator | 1 | 9.77 | **0.002** | 2.11 | 0.147 | 12.85 | **0.0003** |
| Nutrients | 1 | 0.05 | 0.817 | 0.03 | 0.864 | 1.23 | 0.268 |
| Predator × Nutrients | 1 | 4.61 | **0.032** | 2.23 | 0.136 | 7.74 | **0.005** |
| Block | 4 | 8.11 | *0.088* | 15.0 | **0.005** | 30.67 | **<0.0001** |
| **Isopods** | | | | | | | |
| Predator | 1 | 2.47 | 0.116 | 5.51 | **0.019** | 4.49 | **0.034** |
| Nutrients | 1 | 2.98 | *0.084* | 2.06 | 0.151 | 3.25 | *0.071* |
| Predator × Nutrients | 1 | 0.002 | 0.964 | 0.18 | 0.676 | 2.77 | *0.096* |
| Block | 4 | 11.25 | **0.024** | 6.17 | 0.187 | 9.67 | **0.046** |
| **Gastropods** | | | | | | | |
| Predator | 1 | 0.96 | 0.327 | 2.74 | *0.098* | 0.82 | 0.366 |
| Nutrients | 1 | 0.2 | 0.658 | 0.19 | 0.59 | 0.3 | 0.585 |
| Predator × Nutrients | 1 | 0.03 | 0.857 | 0.05 | 0.824 | 0.493 | **0.026** |
| Block | 4 | 7.04 | 0.134 | 4.41 | 0.353 | 19.79 | **0.0006** |

*Bold numbers denote P < 0.05, italic numbers denote P < 0.1.*

Thus, the exclusion of large predatory fish affected amphipods particularly under elevated nutrient conditions, resulting in an amphipod population with smaller individuals and half the total biomass. Isopod abundance decreased when large predators were absent, but did not interact with the nutrient treatment. The gastropod assemblages were not affected at all.

## Discussion



This study shows that top-down control and trophic cascades in a coastal benthic food web depend on the functional composition of both predator and herbivore communities as well as on resource availability. Both predator and nutrient treatment interacted to increase the density of meso-predators, change the composition of invertebrate grazers and increase the biomass of filamentous algae. First, we confirmed earlier results that the removal of larger predators generated a meso-predator release that increased the biomass of filamentous algae (Eriksson et al. 2009), but only under elevated nutrient levels. Second, we also demonstrated that effects of the meso-predator release of small-bodied fish (stickleback) propagated through the food web by shifting the composition of the grazer community towards an increased dominance of gastropod species by reducing amphipod biomass. Thus, we generated cascading effects, where predator declines caused an increased abundance of primary producers, only under elevated nutrient levels. Predator effects on isopods did not interact with the nutrient treatment. Therefore, the decrease in isopods could not be linked to the meso-predator release of stickleback as clearly as the decline in amphipods. The shift in size distribution towards smaller individuals of amphipod grazers indicates a key function of palatability towards the predator species. Together our results show convincingly that top-down control is an important factor for ecosystem structuring and that effects of predator declines on lower trophic levels depend strongly on species-specific relations both within and across trophic levels as well as on resource availability.

Eriksson et al. (2009) showed similarly to our experiment that predator exclusion changed the composition of invertebrates, which was mainly due to an increase in bivalves and a decrease in (small) gastropods. However, other grazers (e.g. amphipods, isopods), that are known to be important food sources for the used meso-predator were not affected by the predator treatment, and we believe that this was due to an inappropriate technique to sample the invertebrate community quantitatively. In contrast, the present study found that the presence/absence of large predatory fish mainly affected amphipods that are palatable to stickleback, which implies, that the grazer response to predation was determined by the palatability of the grazers to specific fish predator species. The palatability of the grazers in this study seemed strongly related to their functional traits. Amphipods possess an exoskeleton. Such chitinous structures enable the animals to develop and grow fast, but at the same time they are relatively fragile (particularly during and shortly after moulting) making them less resistant to predation. In contrast, the gastropods in this study are protected by a shell from calcium carbonate. As a result, gastropods usually grow slowly but possess a good protection against predation, and

particularly *Hydrobia* and *Theodoxus* have a very thick shell. Furthermore, the actual prey size determines the palatability, so that especially large gastropods for instance may be inedible to most meso-predators. We therefore suggest that the effects of the meso-predators on the grazers were mainly determined by the prey's edibility towards the meso-predator. Duffy (2002) showed that palatability is an important mechanism linking diversity and ecosystem functioning, as diverse prey assemblages have a greater chance of containing less edible species. A meta-analysis by Hillebrand and Cardinale (2004) revealed that a more diverse prey assemblage is less vulnerable to consumption even across broad ranges of species diversity and different community types. This suggests that diversity effects on ecosystem processes may not be driven by species richness per se but rather by the functional diversity, for example the prey's edibility to their predators. Despite the fact that the use of functional groups in food web studies is not a new approach (Tilman et al. 1997a), most studies so far that have included functional diversity in assessments of trophic interactions have focused on primary producers and their responses to predation pressure (e.g. Duffy et al. 2001, Lotze et al. 2001). In contrast, studies, like ours, that focus on higher trophic levels are relatively under-represented in the literature (Downing 2005).



Greater meso-predator abundance induced at elevated nutrient levels a shift in grazer composition and simultaneously a greater biomass of filamentous algae. The shift in grazer composition towards gastropods suggests a trade-off between an efficient resource use and the grazers' resistance to predation. Grazers are able to dampen an enhanced growth of opportunistic algae from nutrient enrichment, but only in the absence of their predators (Korpinen et al. 2007b). This effect is expected to be more pronounced when grazers are complementary in their feeding preferences (Råberg and Kautsky 2007b), which suggests a dependency of the grazers' response to both top-down and bottom-up effects on their functional diversity. The amphipods and isopods in this study have a short lifespan and fast reproductive rates (Kolding and Fenchel 1979, Salemaa 1979), which likely enables them to respond more rapidly to ecosystem changes ('dynamic grazers') than gastropod species ('static grazers', from Gruner et al. 2008). Therefore, amphipods and isopods are expected to benefit sooner from an increase in resource biomass following nutrient enrichment (Gruner et al. 2008). Moksnes et al. (2008) showed that elevated nutrient levels induced biomass accumulation in *Gammarus*, and similar effects were shown by Hemmi and Jormalainen (2002) for the isopod *Idotea*, and by Worm and Lotze (2006) for gastropods. Nutrient enrichment enhanced the effect of the predator exclusion on amphipods, which resulted in stronger reduction in amphipod biomass and their according mean individual biomass in the closed enriched cages, suggesting that resource availability may enhance top-down effects. Therefore, top-down and bottom-up forces together affected the grazer composition and both forces could not be regarded isolated. The interplay of both forces implies a trade-off between resistance to predation pressure and the ability to utilise the increased resources that may ultimately be reflected in the grazers' edibility (see Leibold 1989). Furthermore, changes in food web constellations could have mediated changes in interspecific competition between amphipods and isopods such as competing for the same resource or apparent competition (Frid and Marliave 2010) by sharing the same predator. Competition between the grazers could have

potentially caused an artefact of the predator treatment, since perch can consume sticklebacks, but also feeds on isopods (pers. obs.), while stickleback prefers amphipods (pers. obs.). Thus, reduced biomass of amphipods in the closed cages could have also resulted from stronger competition from isopods in the absence of perch. However, isopod abundance also decreased in the closed cages. Thus, there is no support for increased grazer competition from changes in the fish composition.

Bottom-up effects on producers were stronger when large predators were removed. However, the overall very low algal biomass in the ambient cages might have hampered the ability to find statistically significant effects from predator exclusion without adding nutrients. The effect of enrichment on algal biomass might have also been diminished by the grazers, since Russell and Connell (2007) could show that grazers reduced more biomass of algae that were exposed to higher nutrient levels, but only under oligotrophic background conditions. Still, the exclusion of large predators and nutrient enrichment positively interacted to increase the algal biomass by 23 times, implying that a decline of top-predators simultaneous to eutrophication may have multiplying effects on producers. Grazers were able to reduce a substantial part of the increased algal biomass from nutrient enrichment when large predators were present. In contrast, the meso-predator release increased algal biomass through the facilitation of gastropod grazers that are less efficient grazers on macroalgae. Joint effects of top-down and bottom-up forces in marine systems have been described across two trophic levels, where effects of nutrient enhancement on primary producers were stronger in the absence of predators (Burkepile and Hay 2006, Hereu et al. 2008). In this study, we found evidence for synergistic effects of top-down and bottom-up control even across four trophic levels. However, the experimental manipulations of both predators and nutrients were confounded. The number of stickleback around the cages depended not only on the predator treatment, but also on the nutrient treatment (Figure 2.1a). Therefore, this experiment was basically a choice test for stickleback and invertebrate grazers where they could choose among the different treatments. Stickleback preferred cages that not only protected them from larger predators but that were also nutrient enriched. Nutrient enrichment of the water column can affect grazers' nutrient stoichiometry and increase grazer biomass (Liess and Hillebrand 2006, Spivak et al. 2009). Thus, foraging for more and higher nutritious prey in the enriched cages might explain higher stickleback densities, although nutrient effects on grazer biomass were very weak. In general, the results support theoretical models where consumers immigrate and emigrate actively between patches depending on resource availability (Oksanen et al. 1995, Nisbet et al. 1997). In these short-term population dynamic models, increased resource availability stimulates the production of primary biomass in patches with three trophic levels when consumers employ active dispersal and distribute freely (Nisbet et al. 1997).

Cage artefacts could have affected the behaviour of stickleback. Enhanced growth of periphyton on the cage structure and/or inside the cages due to the nutrient enrichment for instance could have attracted more small fish by providing shelter although cages have been brushed off regularly during the experiment. The drawbacks of predator exclosure experiments have been extensively described. For example, they may affect the natural distribution and abundance of predators due to the presence of the cage structure (Steele

1996), or partial cages may underestimate predation effects (Sih et al. 1985) because of the lower accessibility of the predators to the prey. The cage structure may have caused other biotic changes (e.g. lower abundances of phyto- and zooplankton) (Steele 1996) that were enhanced by the nutrient treatment, which may have affected the performance of the predator treatment. Therefore, general conclusions about the effects of predator exclusion and nutrient enrichment might be limited. However, both the grazer composition and the biomass of filamentous algae were affected by the interaction of both treatments. Hence, our results indicate synergistic effects of top-down and bottom-up forces where the effects of the excluding large predators were contingent on the resource availability and vice versa.

We conclude that declines in top-predators in combination with eutrophication may have dramatic impacts on lower trophic levels by generating cascading changes in the composition of grazers. In our study, a meso-predator release shifted the grazer community towards more predator-resistant species, which were less able to counteract the enriched primary production. Significant differences in prey preferences between predators on the grazer community imply that food web changes from a decline in top-predators strongly depend on the species that are exploited and their functional traits. Thus, the functional composition both within and across trophic levels plays a crucial role in determining ecosystem vulnerability to anthropogenic impacts such as exploitation or eutrophication. Overfishing of piscivores can have similar effects on primary producers than eutrophication (Vasas et al. 2007). Therefore, both anthropogenic impacts can synergistically enhance the development of bloom-forming algae, resulting in the loss of ecosystem services, such as water quality and cultural services.



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# Multiple fish predators: effects of identity and density on lower trophic levels

3

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*Marine Ecology Progress Series:* in revision

## Abstract

Experimental studies on multiple predator effects are rare and yet necessary to predict the consequences of the ongoing loss of top predators. In order to test combined effects of both multiple predators and predator density and how they affect lower trophic levels, we employed a field experiment and manipulated fish predators in combination with nutrient enrichment. We created monocultures of *Perca fluviatilis* (perch), *Rutilus rutilus* (roach), and *Gasterosteus aculeatus* (stickleback) as well as mixtures with all species in an additive design and measured the biomass of invertebrate herbivores and algae. Biomass of the key herbivore groups depended mainly on predator identity, while top-down effects on algae were instead mediated by high predator density and nutrient enrichment. Specifically, perch strongly reduced amphipods and isopods; roach mainly reduced gastropods but also isopods, while stickleback had less overall effects on herbivores. These species-specific effects were attenuated in the mixed fish assemblage probably due to prey-switching. However, changes in herbivore biomass were not transmitted to producers, instead algal growth strongly increased from high fish density and nutrient enrichment. This study shows that identity effects from predators in isolation are attenuated in multiple predator assemblages probably due to increasing interspecific interference, which decreases predation pressure on herbivores. Trophic cascading effects on algal biomass depend on nutrient enrichment and total predator density, which affected algae probably through non-lethal effects on the herbivores.

## Introduction

The diversity of ecosystems around the world is subjected to the most rapid and dramatic changes since globalization of the markets started (Lotze et al. 2006). Extinction rates of well-known taxonomic groups are recently 100 to 1000 times of their pre-human levels (Pimm et al. 1995). Particularly coastal marine systems, as focal points for human settlement and resource use (Lotze et al. 2006), are altered by species loss and gain (Mack et al. 2000, Worm et al. 2006). The concomitant changes in species diversity and consequences for ecosystem functioning have raised still ongoing debates (e.g. Worm et al 2006). Adding or removing species changes both species richness and the species composition a community. Studies that compared the importance of richness and composition effects in diversity experiments, often found the latter, also called idiosyncratic effects, to be of larger magnitude (Stachowicz et al. 2007). Thus, the identity of the species that is lost or gained seems to play a key role for predicting the consequences for the ecosystem.



In a food web perspective, the effect of multiples predators on prey removal are often non-additive through either 'risk enhancement' (e.g. diet complementarity or facilitation among predators) or 'risk reduction' (e.g. intraguild predation or omnivory) (see Sih et al. 1998 for a summary). Thus, interactions among the predator species (interspecific as well as intraspecific) also affect food web effects of multiple predators. However, experimental studies showed that interspecific predator effects strongly depend on the predator densities (e.g. Vance-Chalcraft et al. 2004, Griffin et al. 2008, Griffiths et al. 2008). Hence, when testing food web effects of multiple predators both predator identities and their corresponding densities have to be considered, as well as emerging interspecific interference among the predators.

Changes in the predator community can be transmitted via meso-predators and/or herbivores to lower trophic levels and eventually affect primary producers indirectly through a trophic cascade (Pace et al. 1999). Herbivore traits, especially edibility, grazing efficiency and feeding guild, are therefore important mediators of multiple predator effects on lower trophic levels (Stachowicz et al. 2007). The resulting biomass and species composition of the primary producers is ultimately determined by the functional composition of the herbivores combined with the nutrient availability (Råberg and Kautsky 2007). Accordingly, we have shown that the loss of dominant fish predators in the coastal zone of the Baltic Sea has reduced grazing rates on algae by shifting the functional composition of the herbivore community, and that cascading effects on the algae interacted with nutrient enrichment (Eriksson et al. 2009, Sieben et al. 2011b).

In this study, we compare food web effects of multiple predators on the herbivore and algal community with their isolated effects in monoculture, and we examine the roles of predator identity, predator density and nutrient availability for the propagation of multiple predator effects to lower trophic levels. We used three common fish species of the Baltic coastal zone, *Perca fluviatilis* L (European perch), *Rutilus rutilus* (L) (roach) and *Gasterosteus aculeatus* L (three-spined stickleback) (Ådjers et al. 2006), which all have different food preferences (Figure 3.1). Perch is a carnivorous species (macroinvertebrates and fish) and has declined strongly in some parts of the Baltic Sea since the early 1990s

(Nilsson et al. 2004, Ljunggren et al. 2010). At the same time increases of the smaller mesopredator stickleback are observed (Ljunggren et al. 2010, Eriksson et al. 2011). Sticklebacks are facultative planktivores, enabling them to switch between zooplankton and zoobenthos prey. In contrast, roach, as a true omnivore, is able to utilize zoobenthos, zooplankton, plant material and detritus, and can therefore escape interspecific competition with perch (Persson 1987), which may dampen cascading trophic effects. The benthic herbivores are dominated by amphipods, isopods and gastropods. We enclosed the three fish species (perch, roach and stickleback) each in monocultures as well as together in mixed assemblages in an additive design. This design allows to separate effects caused by intraspecific versus interspecific interference, by comparing different density levels within the monocultures.

We hypothesise: (1) that predator identity effects on herbivores emerge in monocultures: we have indications that perch and stickleback mainly predate on amphipods and isopods, and roach on gastropods (Sieben et al. 2011b, and pers. obs.); (2) that interference between the predators emerges in the mixtures, which attenuates effects on herbivores in the multiple predator assemblages compared to the strongest predator in isolation; (3) higher predator density increases prey removal in monocultures as well as in mixed assemblages; (4) and accordingly that algal biomass increases with high predator density and nutrient enrichment.



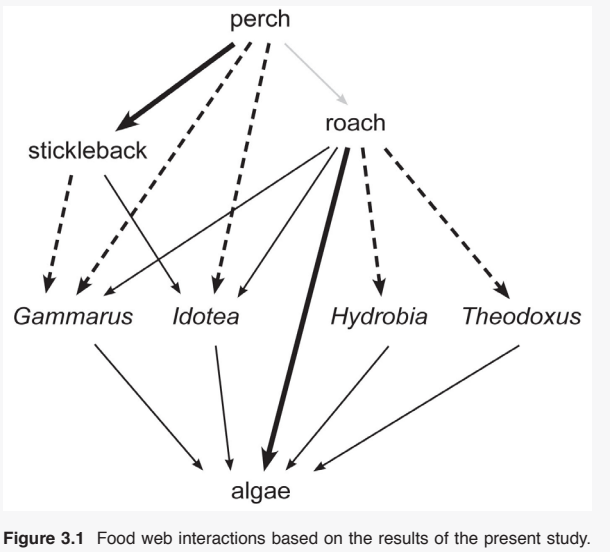


**Figure 3.1** Food web interactions based on the results of the present study. Displayed are changes in food preferences from the fish monocultures compared to the diverse fish assemblages. Consumption either increased (solid bold), decreased (dashed bold) or remained the same (normal line). Note: the arrow from perch to roach indicates non-consumptive interference as observed during the experiment.

## Methods

### Study system and organisms

The study site was located at the inner archipelago of the Askö area (58°48'N, 17°40'E), western Baltic Sea. The site is sheltered and non-tidal, fluctuations in the water levels are mainly wind (or air pressure) driven, water temperature and salinity range from 17-20°C and 6.3-6.5 PSU in summer, respectively (http://www2.ecology.su.se/dbhfj/b1start.htm). The bottom substrate is mainly sand and gravel, scattered with rocks and boulders. The dominating brown algae *Fucus vesiculosus* L (hereafter *Fucus*) is an important habitat provider for diverse invertebrate species and epiphytic algae. Abundant benthic producers apart from *Fucus* are mainly ephemeral green (e.g. *Cladophora glomerata* (L) Kützing, *Ulva* spp.) and brown algae (e.g. *Pilayella littoralis* (L) Kjellman) as well as diatoms (e.g. *Melosira* spp.). The fish community includes both marine and freshwater species, but the latter dominate in the coastal zone. The fish species used in this study include *Perca fluviatilis* L (European perch, hereafter perch), *Rutilus rutilus* (L) (roach) and *Gasterosteus aculeatus* L (three-spined stickleback, hereafter stickleback) – which are among the most abundant fish species in the study area (pers. comm.). Perch is a very common fish often occurring among aquatic vegetation (HELCOM 2006). Perch is strictly carnivorous and undergoes substantial diet shifts during its ontogeny: from feeding on zooplankton over macroinvertebrates to fish (Persson 1987, Lappalainen et al. 2001, Kahl and Radke 2006 and references therein). In its piscivorous stage perch is feeding on e.g. juvenile stages of roach and perch, stickleback (pers. observ.), and crustaceans (Eklöv and Persson 1995, Lappalainen et al. 2001). Roach, as a true omnivore, prefers gastropods and other molluscs but also consumes other zoobenthos, zooplankton, detritus, phytoplankton and macrophytes (Persson 1987, Lappalainen et al. 2001, Kahl and Radke 2006). In contrast to perch, roach uses more similar prey size over the entire life period (Eklöv and Persson 1995). Stickleback is the dominant mesopredator in the system, prefers zooplankton over benthic prey, but as the availability of zooplankton decreases zoobenthos becomes more important (Ibrahim and Huntingford 1989). In the study area, stickleback mainly feed on gammarid amphipods, copepods and larvae of Chironomidae (pers. observ.). The invertebrate herbivore community is dominated by amphipods (*Gammarus* spp., hereafter *Gammarus*), isopods (*Idotea balthica* (Pallas), *Idotea chelipes* (Pallas), hereafter together as *Idotea*) and gastropods (*Theodoxus fluviatilis* (L), *Hydrobia ventrosa* (Montagu) and *Hydrobia ulvae* (Pennant), hereafter *Theodoxus* and *Hydrobia*) that represent two different feeding guilds. Amphipods and isopods are shredders and considered selective omnivores, feeding on filamentous macroalgae and larger plant material, as well as fine detritus, other invertebrates and fish eggs (Salemaa 1987, MacNeil et al. 1997, Sommer 1997, Orav-Kotta and Kotta 2003). Gastropods scrape off mainly diatoms and other microalgae from surfaces but also feed on macroalgal recruits and young thalli of *Cladophora glomerata* (Neumann 1961, Korpinen et al. 2008).

## Field experiment

We tested effects of different fish species and their interactions on the structure of the herbivore community as well as subsequent effects on algal assemblages by enclosing three fish species (stickleback, roach and perch) in cages in the field, both in single-species and mixed assemblages with all species. The fish treatment was based on a simple additive design, i.e. the predator density increased in the mixed assemblages. That implies that the density of each species in mixture is the same as in monoculture, and that total density is greater in the mixtures. With this design it is possible to test whether emergent multipredator effects are due to interspecific interactions (such as competition or resource complementarity) (Snaydon 1991). In additive designs interspecific effects are not confounded with intraspecific effects as in substitutive designs (Jolliffe 2000, Griffiths et al. 2008). However, a drawback of the additive design is that densities in the mixtures increase to unnaturally high levels.



All fish treatments were conducted with three different densities in order to quantify the impact of intraspecific effects. Each density level for each mono- and polyculture was replicated by 2 (= 24 cages). Resulting fish numbers were 2-4-6 individuals of perch and roach, and 15-30-45 individuals of stickleback. Perch had an average length and weight of 14.8 ± 0.3 cm and 35.9 ± 2.9 g (N = 47), respectively, a size which was assumed as sufficient for perch to be piscivorous. Roach had an average length and weight of 15.2 ± 0.3 cm and 41.6 ± 3.3g (N = 47), respectively. Stickleback was used in different total biomass as perch and roach due to very low individual body weight of stickleback (1.8 ± 0.5 g, N = 360). Therefore, we chose numbers appropriate for forming schools. The resulting biomass ratio between perch/roach and stickleback assemblages was approximately 3:1.

The cages (120 × 55 × 100 cm, length × width × height) were steel-framed and covered with a nylon fishing net (mesh size 6 mm). The treatments were randomly distributed in shallow water (1.2 m deep) in a sheltered bay. Nutrient enrichment was applied to half of the cages (= 2 levels) by slow-release agricultural fertilizer (Plantacote Depot 6M) filled in four net bags (120 g fertilizer in each bag) attached to the cage frame. The same amount of fertilizer applied to identical cages in the same bay resulted in ~ 60% increase of total phosphorus and ~ 140% increase of total nitrogen compared to the ambient nutrient level (Sieben et al. 2011b). The experiment ran for three weeks from 12 July to 3 August 2008. The experiment was performed without controls that would have provided 'natural' (caged) densities of herbivores and algae. However, in this experiment it was more important to measure relative differences of predation effects of the three fish species and compare them to their combined effect in a mixed assemblage.

Specimens of *Fucus* were used as habitat and sampling unit for the invertebrate communities. The *Fucus* was collected close to the study site, cleaned from invertebrates and epiphytes, tied to bundles of approximately 200 g wet weight and kept in outdoor tanks for a few days prior to the start of the experiment. Three *Fucus* bundles were used in each cage. At the end of the experiment, the invertebrates were collected by pulling a net bag over the *Fucus* enclosing all the associated fauna under water. Algal growth was examined on two ceramic tiles glued on bricks in each cage. The bricks were placed on the

bottom of the cages in a minimum distance of 20 cm to the *Fucus* bundles as well as to the netting of the cage.

At the end of the experiment, fish total length and biomass were measured, and the stomachs were removed and frozen for later analyses. Invertebrates as well as algae were preserved deep-frozen. In the lab, invertebrates were rinsed off the *Fucus*, sorted into species, counted and dry weighed (60°C for a minimum of 48 h). Dry biomass was converted into ash-free dry weight and shell-free dry weight with the use of conversional factors (Lappalainen and Kangas 1975). In the data analyses, the dominating species of the herbivore groups amphipods (*Gammarus* spp.), isopods (*Idotea* spp.) and gastropods (*Hydrobia* spp. and *Theodoxus fluviatilis*) were used.

Algae were scraped off from the surface of the tiles and dry weighed (80°C for a minimum of 48 h). The algae were dominated by ephemeral green algae where *Cladophora glomerata* made up 74% of the total biomass.

The invertebrate samples taken inside the cages were used as the main response (for statistical analyses), because only these (remaining) herbivores could transmit predation effects further to the producers level. Additional to the measures of herbivore biomass inside the cages we used stomach analyses to estimate the amount herbivores and other sources contributed to their diet.



## Statistical analysis

In each cage, two algae and three invertebrates samples were taken. The treatments were fish assemblage with four levels (perch, roach, stickleback, all), fish density with three levels (low, medium, high), and nutrient availability with two levels (ambient, enriched), which were all included as fixed factors. Cage number was included as a random factor. First, we compared models including the random factor (Linear Mixed-Effects, LME, nlme-package (Pinheiro et al. 2013)) with models including only fixed factors (Generalized Least Squares, GLS, nlme-package) for each of the response variables, and chose between the two depending on the goodness of model fit (via AIC). For the response variables '*Gammarus* biomass', '*Idotea* biomass' and '*Theodoxus* biomass' GLS models were applied, for '*Hydrobia* biomass' and 'Algal biomass' LME models were applied. GLS models are able to handle heterogeneity of variances by defining specific variance structures to the models (Zuur et al. 2009). Therefore, we could omit data transformations for GLS models. For the GLS models, we chose the optimal variance structure (*varIdent*) depending on graphical plot validation (standardized residuals vs. fitted values). Similarly, the optimal random part for the LME models was chosen.

Starting from the full model (excluding 3-way interaction because of no replication), model simplification was performed to find the optimal fixed components of all models. Thus, after defining the full model for each response variable stepwise model selection was used in order to select the minimum adequate model (see Zuur et al. 2009 for the entire statistical procedure). When treatment effects were significant pairwise-t-tests (stats-package) were applied including Bonferroni-corrections (same package) to correct for multiple comparisons. Specific planned comparisons (contrast-package (Kuhn 2011)) with

Bonferroni-corrections were used to detect sources of variance differences from significant interactions.

All analyses were conducted using R version 2.15.2 (R Development Core Team, 2012).

## Results

### Predator and nutrient effects on grazers

Perch was the strongest predator on *Gammarus*. In monocultures, perch reduced *Gammarus* biomass by 71% compared to the stickleback assemblages, which had the highest *Gammarus* biomass (Figure 3.2a, Table 3.1). The strong predation effect of perch



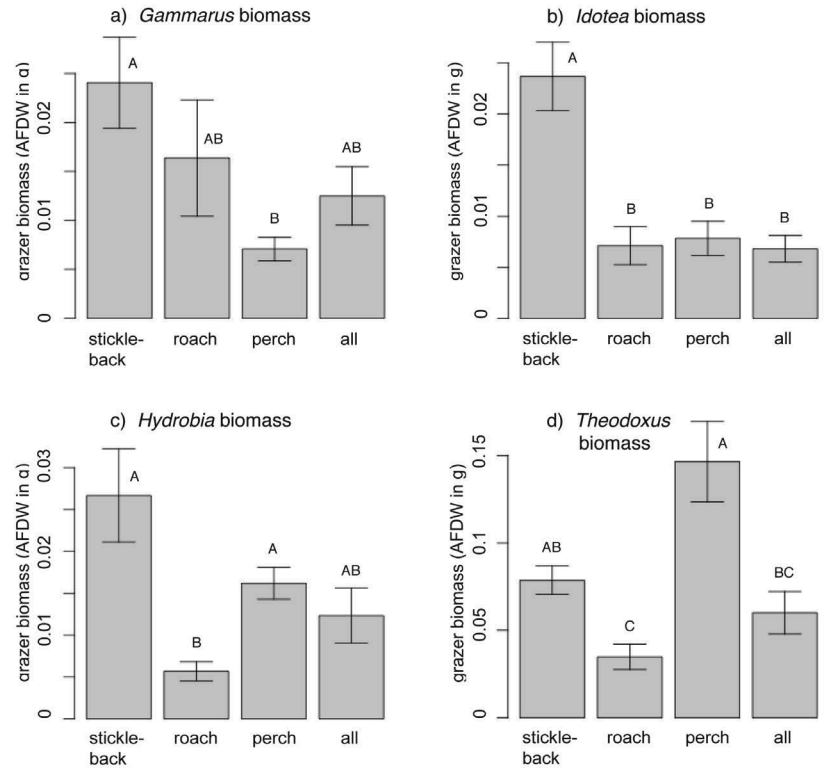


**Figure 3.2** Biomass of (a) amphipods (*Gammarus*), (b) isopods (*Idotea*), and the gastropods (c) *Hydrobia* and (d) *Theodoxus* in the different fish enclosures. 'Stickleback', 'perch' and 'roach' denote the respective species in monoculture; 'all' denotes the polyculture of all fish species. Different letters indicate significant differences ($P < 0.05$) from post-hoc tests. Values are mean ± SE.

was reduced in the mixed assemblages: perch and stickleback monocultures (P = 0.021) were significantly different, but mixed assemblages and stickleback monocultures were not (P = 0.375). Moreover, *Gammarus* biomass was on average 19% lower in the nutrient enriched assemblages (ambient: 0.0166 ± 0.0031 g, enriched: 0.0134 ± 0.003 g, mean ± SE, Table 3.1).

The biomass of the isopod *Idotea* was equally reduced in perch and roach monocultures as well as in the mixed assemblages to 31% compared to the stickleback monocultures (Figure 3.2b, Table 3.1). *Idotea* biomass was also significantly affected by fish density. More specifically, *Idotea* biomass was significantly higher when fish density increased from medium to high (post-hoc test: P = 0.039). This was mainly due to changes in the stickleback and roach monocultures (contrast on fish : density, t = 3.25 and P = 0.008 for stickleback, t = 2.62 and P = 0.044 for roach).

In contrast to amphipods and isopods, gastropod species were strongly reduced in monocultures of roach. Biomasses of both *Hydrobia* as well as *Theodoxus* were significantly lower in the roach monocultures compared to the other monocultures (post-hoc tests: stickleback-roach P = 0.019 and perch-roach P = 0.0004 for *Hydrobia*, stickleback-roach P = 0.009 and perch-roach P = 0.002 for *Theodoxus*, Figure 3.2c and d). Similarly to *Gammarus*, the strong predation effect from the monoculture was reduced in the mixed assemblages (in contrast to roach monocultures, mixed assemblages were not significantly different from the other monocultures except for one, Figure 3.2c and d). However, gastropod biomass in the mixed assemblages was not significantly different from the roach monocultures (post-hoc tests: P = 0.312 for *Hydrobia*, P = 0.276 for *Theodoxus*, Figure 3.2c and d).

**Table 3.1** Statistical analysis of variances of invertebrate biomass and algal biomass from Generalized Least Squares (GLS) models or Linear Mixed Effect (LME, * indicated) models after model selection.

| Response variable | Df | F-value | P-value |
|---|---|---|---|
| ***Gammarus* biomass** | | | |
| Fish | 3 | 5.37 | **0.002** |
| Nutrients | 1 | 4.05 | **0.048** |
| ***Idotea* biomass** | | | |
| Fish | 3 | 12.88 | **<0.0001** |
| Density | 2 | 3.88 | **0.026** |
| Fish × Density | 6 | 3.39 | **0.006** |
| ***Hydrobia* biomass*** | | | |
| Fish | 3 | 7.26 | **0.011** |
| Nutrients | 1 | 4.27 | *0.073* |
| Density | 2 | 0.87 | 0.454 |
| Fish × Nutrients | 3 | 2.89 | 0.102 |
| Fish × Density | 6 | 2.20 | 0.149 |
| ***Theodoxus* biomass** | | | |
| Fish | 3 | 59.09 | **<0.0001** |
| Nutrients | 1 | 0.36 | 0.552 |
| Density | 2 | 3.11 | *0.053* |
| Fish × Nutrients | 3 | 4.55 | **0.006** |
| Fish × Density | 6 | 8.80 | **<0.0001** |
| **Algal biomass*** | | | |
| Fish | 3 | 0.80 | 0.521 |
| Nutrients | 1 | 20.41 | **0.001** |
| Density | 2 | 11.69 | **0.002** |
| Fish × Density | 6 | 2.03 | 0.146 |

*Bold numbers denote P < 0.05, italic numbers denote P < 0.1.*

Furthermore, gastropod biomass was affected by nutrient enrichment. *Theodoxus* biomass was significantly higher in the enriched assemblages but depending on fish composition. Specifically, in the monocultures of stickleback, *Theodoxus* aggregated in higher biomasses under elevated nutrient levels (contrast on fish : nutrients, t = 2.98, P = 0.017). Similarly, *Hydrobia* showed a trend towards higher biomass in enriched assemblages (P = 0.073, Table 3.1). Fish density affected the biomass of *Theodoxus* but not *Hydrobia*. Fish density, particularly from medium to high density, affected *Theodoxus* biomass (P = 0.053, Table 3.1) across all fish assemblages. Particularly in the mixed assemblages, high fish density significantly decreased *Theodoxus* biomass (contrast on fish : density (medium to high), t = 3.04, P = 0.014).
Hence, fish predators had clear species-specific effects on herbivore biomass (*Gammarus* was reduced in the perch monocultures, *Idotea* in the monocultures of roach and perch, *Hydrobia* and *Theodoxus* were mainly reduced in the roach monocultures). For three of the four herbivore groups, these predator-specific effects were attenuated in the mixed fish assemblages, despite equal densities of the respective main predator. Fish density had overall weak effects on herbivores. However, *Theodoxus* biomass decreased significantly with high fish density in the mixed fish assemblages. Nutrient enrichment decreased the biomass of *Gammarus* but increased the biomass of gastropods.



## Predator and nutrient effects on algae

Total biomass of filamentous algae was strongly affected by fish density and nutrient enrichment (Figure 3.3, Table 3.1). In contrast to herbivores, algal biomass was not affected by fish composition. Increasing fish density caused a 6 times higher algal growth (low density: 0.003 ± 0.0008, medium density: 0.003 ± 0.001, high density: 0.0175 ± 0.0046, g $dm^{-2}$, mean ± SE), which was clearly apparent in all fish treatments except for

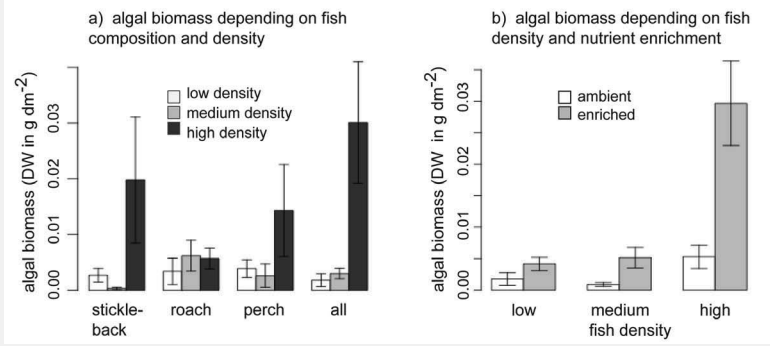


**Figure 3.3** Biomass of ephemeral macroalgal depending on (a) fish assemblage and fish density and (b) fish density and nutrient enrichment. 'Stickleback', 'perch' and 'roach' denote the respective species in monoculture; 'all' denotes the polyculture of all fish species. Values are mean ± SE.

the monocultures of the omnivorous roach (Figure 3.3a). However, there was no significant interaction effect of fish composition and density (Table 3.1). Nutrient enrichment increased algal biomass 5-fold (ambient: 0.0027 ± 0.0008, enriched: 0.013 ± 0.0033, g $dm^{-2}$, mean ± SE, Table 3.1) in all fish assemblages. Thus, both high fish density and nutrient enrichment strongly increased algal biomass, but fish composition had no significant effect on algal growth.

## Stomach analyses

Stomach content analyses supported that the reduced predator-specific effects in the mixed fish assemblages depended on prey-switching. Perch consumed mainly amphipods (Figure 3.4a/f) and isopods (Figure 3.4b/g), which made up to 29% and 22% of their stomach content. In mixed assemblages, however, perch also consumed substantial amounts of unique food items, stickleback and decapods, which added up to 43% and 26% of their stomach content in the mixtures. At the same time, the amount of isopods was reduced in the diet of perch in mixtures (Figure 3.4g). Thus, perch partly switched to feeding on stickleback (intraguild predation) when available. Roach consumed mainly amphipods (Figure 3.4a/f), isopods (Figure 3.4b/g), gastropods (Figure 3.4c/h) and algae (Figure 3.4e/j). Roach consumed three times more algae when kept in high densities (Figure 3.4e) and five times more in the mixed assemblages (Figure 3.4j), supporting the hypothesis that roach switches prey when competition increases. In addition, the roach stomachs contained large amounts (on average 38%) of unidentifiable organic material with greenish coloration indicating algae in a partly digested stage. This unidentifiable organic material was found in particularly large amounts in stomachs of roach from nutrient enriched assemblages and from mixed assemblages, suggesting that at least parts of this organic material were algae and indicating the ability of roach to consume large amounts of algae. Stickleback mainly consumed amphipods (Figure 3.4a/f) and zooplankton (mainly copepods and ostracods, Figure 3.4d/i), each adding up to 41% of the stomach content. In the mixed fish assemblages, the biomass of amphipods (Figure 3.4f) and bivalves (Figure 3.4h) in the stomachs of stickleback decreased together with their stomach fullness (from 47% to 36%) compared to the monocultures.

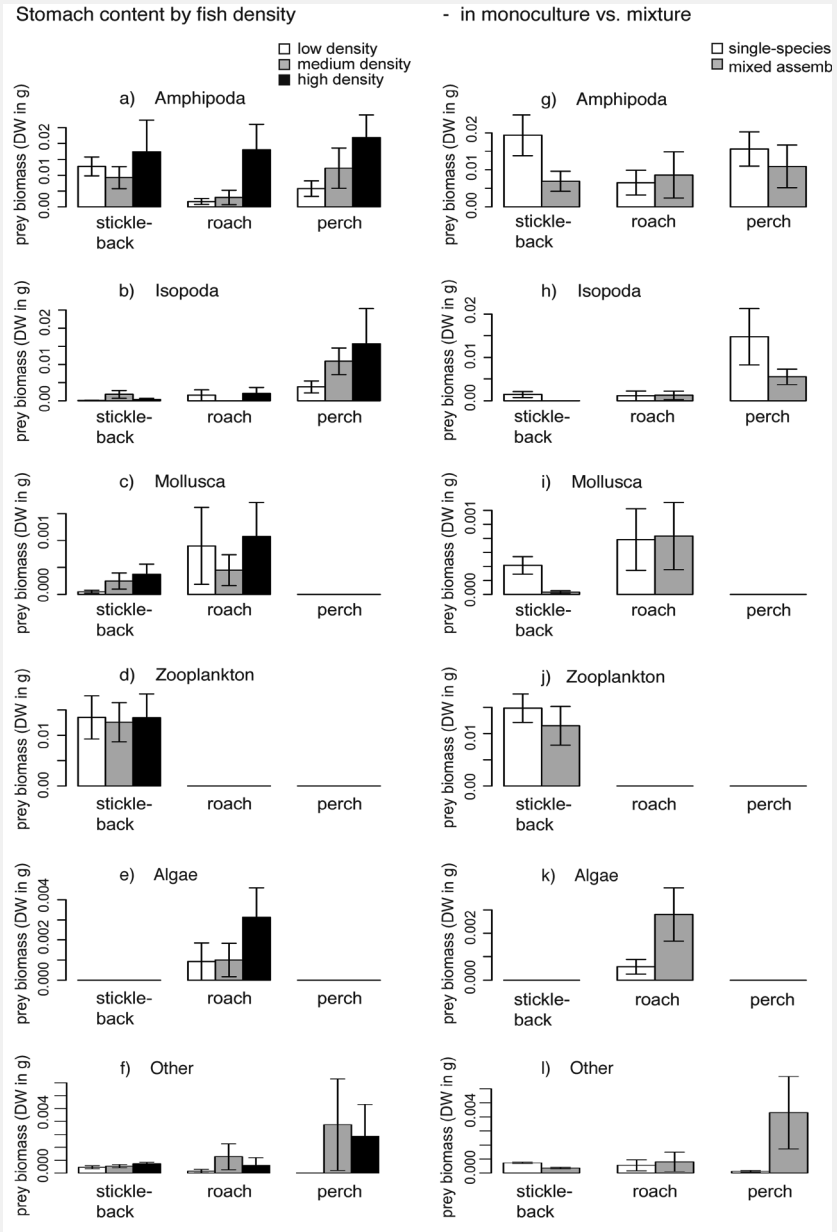


**Figure 3.4** Groups of prey (in g DW per stomach) in the stomachs of stickleback, roach and perch. Left column: depending on fish density (averaged over other treatments). Right column: in monocultures and mixed assemblages (averaged over other treatments). Values are mean ± SE.

## Discussion

We demonstrated that predators had strong identity effects on herbivore assemblages in monoculture: perch mainly reduced *Gammarus* and *Idotea*, roach mainly reduced *Idotea* and gastropods, each in comparison to the other monocultures (in line with hypothesis 1). When multiple predators were assembled together the removal of three of the herbivore groups (*Gammarus* and both gastropods) was reduced (in line with hypothesis 2). Predator density had no uniform effects on herbivores (in contrast to hypothesis 3). Only in three assemblages, fish density affected herbivores: *Idotea* biomass increased in two high-density monocultures, and *Theodoxus* was strongly decreased with high predator density in the multiple predator assemblages. Predator identity effects on the herbivores were not transmitted to affect the producers. Instead, a strong increase in algal growth was generated by high fish density and nutrient enrichment (in line with hypothesis 4). The strong indirect effect of high fish density on algal biomass with no according changes in the herbivore composition suggests that non-lethal interactions may have mediated top-down effects.



Species-specific predation on the herbivores by both perch and roach declined in the mixed fish assemblages (Figure 3.1). The results indicate that interspecific interference among the predators reduced removal of the key herbivore groups through prey-switching. Predators can reduce interference with other predators by changing the feeding mode and/or the foraging habitat (Crowder and Cooper 1982, Werner et al. 1983). Perch stomachs from the monocultures almost exclusively contained amphipods and isopods, while in the mixed fish assemblages they fed to a substantial amount on mesopredators (stickleback and shrimp), food items that are probably more profitable in terms of their nutritional and energy content than the herbivores. In contrast, roach switched to a less efficient food source, algae, when kept in mixed assemblages. Stickleback, when kept in mixed assemblages, removed less of its main food item in monoculture (amphipods), but did not compensate through alternative exploitation and fed generally less (stomach fullness decreased by 11%) in presence of its own predator perch. This suggests that the prevalence of identity effects in a multiple predator assemblage, as observed from single species in isolation, depends on interference among these species. That means that particularly competitively inferior species may switch to alternative resources when prey density is low. Multiple predators increase the likelihood of competition and intraguild predation. Intraguild predation is common, particularly when predators embrace different size classes, and can have strong positive effects on their prey, e.g. in marine benthic communities (Polis et al. 1989, Polis and Holt 1992, and references therein). Thus, multiple predators can lower the total impact on the prey (Soluk 1993) and reduce the strength of trophic cascading effects (O'Connor and Bruno 2009). Furthermore, omnivorous predators (such as roach) can avoid competition by exploiting basal resources. Therefore, including an omnivore in a multiple predator assemblage is also likely to reduce predation on prey herbivores. However, including an omnivore can, at the same time, have negative effects on the producers by directly removing significant amounts of algae (Bruno and O'Connor 2005). Accordingly, stomachs of roach contained more algal food when they were kept in mixed assemblages (monoculture: 4%, mixed: 13% of the stomach

content). Thus, multiple predator assemblages can reduce the total predation on herbivores due to increasing interference with positive effects on algae. However, including an omnivore in this assemblage increases direct consumption of algae by the omnivore predator, which could override top-down effects from predators.

Effects of fish density on herbivores were less pronounced than effects of fish composition. High predator densities in the mixtures reduced *Theodoxus* to lower biomass than in monocultures of roach (their strongest predator), although roach occurred in both treatments in the same numbers. In contrast, *Idotea* biomass increased with high predator densities in two of the monocultures. However, predator density had strong positive effects on algal growth. Particularly high density of fish had similar effects as nutrient enrichment on the biomass of filamentous macroalgae. This may indicate that fish density reduced the grazing activity of herbivores through non-lethal effects. Such (trait-mediated) indirect interactions are facilitated for example by predator cues or chemicals from crushed conspecifics (Behrens Yamada et al. 1998, Van Buskirk & Arioli 2002) and have the potential to induce cascading effects (Werner and Peacor 2003, Schmitz et al. 2004). Such anti-predator responses can be changes in behaviour, morphology, physiology or life history of prey and they usually trade-off with foraging activities (Turner 2004). Furthermore, anti-predator responses correlate with predator density (Teplitsky et al. 2005). Thus, higher predator densities likely induce a lower grazing activity (and a reduced energy intake). However, predator effects on herbivores were weak across almost all density treatments. This suggests that predation risk for prey was high in all assemblages. Refuges for herbivores were available in all cages but at the same time, predators were also always present. Thus, herbivores had always a high risk of predation when they emerged to forage. A comparison with natural fish densities is difficult since almost no data exist. However, predators are usually very mobile and forage over much larger spatial scales than the size of the cages. Therefore, we assume that prey predation risk was very high and that herbivores strongly reduced their grazing activity to escape predation. We also suggest using much larger cages when enclosing a fish predator in order to mimic more natural predator densities for trophic effects. An alternative explanation would be the increasing interference with high predator density. Specifically in the mixed assemblages, predator density increased to high levels due to the additive design. Strong interference likely emerged from high predator density with positive effects on predation on herbivores (Sih et al 1998).

This experiment tested food web effects of three fish predator species in isolation and in a multiple predator assemblage at three different levels of predator density. The predator manipulations were further combined with nutrient enrichment in half of the assemblages in order to separate cascading top-down effects of predators from effects of systems productivity on producers. The experiment ran comparatively long (3 weeks). However, there was no full replication for all treatment combinations (sub-samples replicated each cage). Therefore, three-way interactions were excluded from the statistical models, and specifically interactive effects of the nutrient treatment with one of the fish treatments have to be treated with caution (only for *Theodoxus*). However, the treatment combination of fish composition and density were replicated by two, which was assumed to be sufficient considering the effort for such an experiment.

Ecosystems all over the world are affected by multiple anthropogenic stressors that can interact in non-additive ways (Crain et al. 2008). Functional extinctions of species in food webs are biased towards higher trophic levels (Byrnes et al. 2007), emphasizing the need to understand trophic interactions starting from the predator level. Our results indicate that identity effects of predators in a multiple predator assemblage are altered depending on the interference among the predators. Prey-switching occurred likely as a result to escape interspecific interference. Predator density had overall only weak effects on herbivore biomass. However, predator density had positive effects on algal growth (similar to effects of nutrient enrichment) without the according changes in herbivores. This is indicative of either non-lethal effects on herbivores, for instance reduced grazing activities, or strong interference among the predators, which reduced predation pressure on herbivores.

Thus, predator density rather than predator composition strongly affected algal growth, probably because of non-lethal effects on herbivores and increasing predator interference specifically in the mixed assemblages. This suggests that predator density may have stronger effects than fish composition in a food web, particularly on lower trophic levels through non-lethal effects on herbivores.



## Acknowledgments

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# Omnivory and grazer functional composition moderate cascading trophic effects in experimental *Fucus vesiculosus* habitats

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## Abstract

We tested the relative strength of direct versus indirect effects of an aquatic omnivore depending on the functional composition of grazers by manipulating the presence of gastropod and amphipod grazers and omnivorous shrimp in outdoor mesocosms. By selectively preying upon amphipods and reducing their abundance by 70–80%, omnivorous shrimp favoured the dominance of gastropods. While gastropods were the main microalgal grazers, amphipods controlled macroalgal biomass in the experiment. However, strong predation on the amphipod by the shrimp had no significant indirect effects on macroalgal biomass, indicating that when amphipod abundances declined, complementary feeding by the omnivore on macroalgae may have suppressed a trophic cascade. Accordingly, in the absence of amphipods, the shrimp grazed significantly on green algae and thereby suppressed the diversity of the macroalgal community. Our experiment demonstrates direct consumer effects by an omnivore on both the grazer and producer trophic levels in an aquatic food web, regulated by prey availability.

## Introduction

Declines in marine top-predators and subsequent increases in mesopredators, including both medium-sized fish and crustaceans, are global phenomena that have shifted the trophic structure of many benthic and pelagic systems (Worm and Myers 2003, Daskalov et al. 2007, Myers et al.2007, Casini et al. 2008, Eriksson et al. 2009). Such marine mesopredator release events may generate decreases in grazers/herbivores and cascading increases in primary producers (Scheffer et al. 2005, Vasas et al. 2007, Heithaus et al. 2008). However, this often assumes strong predator-prey interactions over discrete trophic levels, while many mesopredators are omnivores that consume both secondary and primary producers and thereby can act both as mesopredators and grazers. Thus, there is an urgent need to document the different roles of omnivores in aquatic food webs to predict effects of changes in higher trophic levels.

Current interpretations of food web dynamics strongly indicate that omnivory - feeding on more than one trophic level - can stabilize complex food webs (Polis and Strong1996, Fagan 1997, McCann et al. 1998, Neutel et al. 2002). The stabilizing effect of omnivory is supported by ecological models and mathematical analyses of real food webs, both of which show that omnivores dampen strong synchronous fluctuations in population sizes by introducing many weak trophic links (McCann et al. 1998, Neutel et al.2002). As an increase in the number of trophic links dilute direct effects of single-species groups through the food web (Polis and Strong 1996), experimental food webs with a higher degree of omnivory are less sensitive to disturbances (Fagan 1997).



The contribution of omnivores to predator guilds, therefore, is important in determining how effects of species loss at higher trophic levels cascade down the food web (Polis and Strong 1996, Duffy et al. 2007). Declines in apex predators can generate trophic cascades, whereby concomitant increases in mesopredator communities indirectly favour primary producers (e.g. Frank et al. 2005, Casini et al. 2008, Eriksson et al. 2009). Increased omnivory in the mesopredator trophic level may weaken trophic cascades, because omnivores may produce opposing direct and indirect impacts on lower trophic levels (Polis and Strong 1996, Pace et al. 1999, Ho and Pennings 2008). For example, omnivores that feed both on animals and plants/algae may decrease the strength of trophic cascades from predators to primary producers, by switching to grazing when herbivore abundances decline. This was demonstrated in a rocky shore mesocosm experiment, where strong trophic cascades triggered by carnivorous predators were dampened when omnivores were added to the experiments (Bruno and O'Connor 2005). Thus, omnivores may stabilize food webs exposed to loss of apex predators by preventing mesopredator-release events from cascading down the food web. However, by being less dependent on fluctuations in one single prey population, omnivores can survive on alternative foods when the preferred prey is scarce and thereby exert more persistent top–down control (Polis and Strong 1996). Omnivores also have simultaneous direct negative effects both on consumers and producers since they can act both as predators and grazers (Diehl 1993, Ho and Pennings 2008), indicating that increases in omnivore populations may have even stronger vertical effects on food webs than carnivores. Thus, because of the interplay between direct

consumption and indirect positive effects, net trophic effects of omnivores are difficult to predict and probably highly dependent on prey community composition.

The aim of this study was to test the relative strength of direct versus indirect effects of an omnivorous shrimp, *Palaemon elegans* Rathke, depending on prey composition in a three-step benthic food web created in mesocosms using invertebrate grazers and algae from the Baltic Sea (Figure 4.1). *Palaemon* spp. feed significantly on both crustacean mesograzers (small and mobile peracarid crustacean herbivores such as amphipods and isopods) and filamentous macroalgae (Matthiessen et al. 2007, Jephson et al. 2008, Persson et al. 2008). In the same study system, Råberg et al. (2007b) demonstrated that the functional composition of this grazer community determines algal community composition: gastropods control microalgal production and crustacean mesograzers mainly control macroalgal production. In the present experiment, we specifically test how omnivore effects interact with grazer identity, by manipulating the presence of the omnivore and the functional groups of grazers. We hypothesized that omnivore predation in our study system generates stronger direct than indirect effects on the algal community. Thus, that *Palaemon* does not induce a trophic cascade by reducing the grazers, but instead may compensate for declining abundances of grazer prey by significantly consuming both the grazer and algal trophic levels.

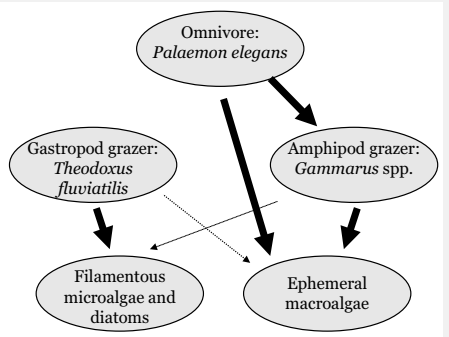


**Figure 4.1** Experimental food web. Arrows show the relative importance of feeding relations, based on (Matthiessen et al. 2007; Råberg and Kautsky 2007b; Jephson et al. 2008; Persson et al. 2008).

## Methods

We conducted the mesocosm experiment at the Askö Laboratory (58°49'N, 19°39'E) in the western Baltic Sea from 4 July to 4 August 2008. The Baltic Sea is brackish with minimal tides, and the only large, habitat-forming, perennial algae growing in the study area is *Fucus vesiculosus* L (hereafter *Fucus*). In this experiment, we studied the ephemeral micro- and macroalgae and invertebrate community associated with *Fucus*, while *Fucus* itself was used as foundation habitat only. *Palaemon elegans* (hereafter *Palaemon*) was the dominant invertebrate omnivore in the area (Råberg and Kautsky 2007a). Isotope analyses suggest that it mainly consumes amphipods/isopods or ephemeral macroalgae, depending on the structure of the prey community (Jephson et al. 2008). The short-lived (~1 year) amphipod *Gammarus* spp. (hereafter *Gammarus*) was the most common crustacean grazer found in the community associated with *Fucus*. *Gammarus* reproduces continuously from spring to

autumn and eggs hatch within 5–15 days (Kinne 1960). Because of its rapid reproduction, *Gammarus* should respond to changes in producer abundance (indicative of a 'dynamic' grazer) (Gruner et al. 2008). The snail *Theodoxus fluviatilis* (L) (hereafter *Theodoxus*) was the most common gastropod in the area (Råberg and Kautsky 2007a). It is comparably longer-lived (2–3 years), and as eggs need approximately 3 months to hatch (Kirkegaard 2006), population sizes are likely to change more slowly (static) than *Gammarus*. Epiphytes on *Fucus* are dominated by a mix of ephemeral cyanobacteria, microalgae (mainly diatoms and uniseriate green algae) and macroalgae (brown, green and red branched filamentous or sheet-like algae).

Specimens of *Fucus* of similar size and appearance were collected from the same area near the laboratory at a depth of 0.5 m. After removing visible fauna by hand, *Fucus* thalli were anchored to separate bricks with plastic ties and placed together for 5 days in a holding tank. By placing all *Fucus* thalli together, we allowed for exchange of invertebrate fauna between the thalli. Since all fauna cannot be removed from the *Fucus* thallus without a strong mechanical disturbance, this was important to homogenize the background start-up community in the experiment. Each thallus weighed ~ 300 g wet mass and had no visible epiphytes.

At the start of the experiment, one *Fucus* brick was randomly extracted from the common holding tank and placed in each of 40 circular, 30 l plastic containers (the mesocosms) standing outside and near to the shore. Although we specifically selected *Fucus* thalli that were free from visible epiphytic growth for the experiments, natural *Fucus* individuals frequently harbour a rich flora of microscopic propagules of ephemeral micro- and macroalgae. This propagule bank enhances growth of filamentous algae many times compared to sterile artificial substrates (Lotze et al. 2001, Eriksson et al. 2006a). We utilized the propagule bank to get a faster response of the algal community in the mesocosms. *Fucus* is also a natural habitat for the invertebrate fauna in the area, promoting natural behaviour in the mesocosms. The cylindrical containers were supplied with a constant flow (ca. 1 l/min) of sand-filtered seawater pumped from the shore near the laboratory. Salinity and water temperature inside the containers were 6.9 PSU and 18 ± 2 °C (observations at 14:00, maximum temperature in any container 19.8 °C, air temperature of 27 °C), respectively, corresponding to the natural conditions measured at the field station (unpublished data).

The experiment was designed as a factorial test of omnivore presence or absence (2 levels) and a simple diversity gradient in grazer community composition (4 levels), with 5 replicates per treatment placed in a randomized block design (40 mesocosms). For the omnivore treatment, we added three individuals of *Palaemon* (total body length = 40–50 mm) to half of the containers, which corresponded to the average number found per *Fucus* thallus in the field (unpublished data). To each omnivore treatment (no omnivore/omnivore present), four different grazer treatments were applied: (1) no grazers, (2) 500 individuals of the gastropod *Theodoxus* in a single-species assemblage, (3) 50 individuals of the amphipod *Gammarus* in a single-species assemblage and (4) 250 *Theodoxus* + 25 *Gammarus* in a "both grazers present" treatment. The grazer treatments corresponded to < 1 g shell-free dry mass per mesocosm, equivalent to natural levels of

shell-free biomass of grazers in the sampling area (Råberg and 2007a). In the both grazers present treatment, the abundance ratio between *Gammarus* and *Theodoxus* (1:10) corresponded to a biomass ratio of 1:1 shell-free dry mass and was similar to the composition in the field (unpublished data). Natural populations of *Gammarus*, *Palaemon* and *Theodoxus* were collected on the same day as the experiment started and from the same area as the *Fucus* thalli. We picked experimental individuals at random, and for the grazers, we excluded individuals < 5 mm. Ten per cent of the initial abundance of *Gammarus* was added twice during the experiment in order to compensate for an observed natural mortality of this species in summer (dead individuals floating at the surface).

Three weeks into the experiment (26 July), we visually estimated for each mesocosm the percentage cover of a thick growth of algae that developed on the water surface (colony forming diatoms). At the end of the experiment (after 31 days), a net bag (mesh size of 500 µm) was placed over each *Fucus* plant and attached algae (filamentous microalgae and cyanobacteria) were removed from the mesocosm sides. Water from the mesocosm was then filtered through a 300 µm sieve, retaining grazers and free-floating algae. All material was immediately frozen at -20 °C. After defrosting, epiphytic algae on *Fucus* were easily removed by careful scraping, and all material was again sieved through a 300 µm sieve. We sorted the algae into three categories: (1) "attached microalgae" consisting of cyanobacteria and filamentous uniseriate microalgae that grew both epiphytically on *Fucus* and on the mesocosm sides, (2) "ephemeral macroalgae" that grew epiphytically on *Fucus* and were sorted to species level (*Ceramium tenuicorne* (Kützing) Waern, *Cladophora glomerata* (L) Kützing, *Dictyosiphon foeniculaceus* (Hudson) Greville, *Pylaiella littoralis* (L) Kjellman and *Ulva* spp.) and (3) "colony forming diatoms" that grew free floating in the mesocosms (mainly of the genus *Melosira*). The diatom colonies disintegrated during freezing into smaller fragments, which easily passed through the second sieving. The colony forming diatoms were therefore obtained by allowing the water that passed through the sieve to settle for 2 days; the supernatant was then aspirated and filtered through grade 595½ filters (mesh size 4–7 µm). All algae and invertebrates were dried at 80 and 60 °C, respectively, for 3 days. Biomass of the ephemeral macroalgae, which only grew on the *Fucus*, was recalculated to grams of dry mass per 100 g dry mass of *Fucus*.

Experimental effects on the biomass of the canopy forming diatoms, attached microalgae and ephemeral macroalgae, and the numbers of the added grazers (*Theodoxus* and *Gammarus*) and alternative prey (other invertebrate species: small gastropods, isopods and copepods) were analysed with factorial ANOVAs, with omnivory and grazer treatments as fixed factors and the block factor as main random effect. Predation effects on *Gammarus* and *Theodoxus* were only tested for grazer treatments where the specific grazer was added. Data were square-root transformed if necessary to meet the assumptions of homogeneous variances. We analysed the diversity of ephemeral macroalgae expressed as the Shannon-Wiener index using a Generalized linear model with a log-link function (Wald statistic), since the distribution did not fit the normal distribution well, even after transformations. The block factor was removed from the statistical models where block P-values > 0.5. Experimental effects on the species composition of macroalgae were analysed with a MANOVA. For algal variables with significant grazer effects (in ANOVA), we

calculated effect sizes ($\acute{\eta}^2$) for planned comparisons to test the relative strengths of grazer presence (grazer present or not) and grazer complementarity (*Theodoxus* vs. *Gammarus*, both grazers present vs. only *Theodoxus* or only *Gammarus*). For variables with significant omnivore effects, we calculated effects sizes ($\acute{\eta}^2$) for planned contrasts to test the relative strength of direct and indirect effects of omnivore presence (omnivore effects in grazer treatments without and with *Gammarus*, respectively).

There are possible artefacts associated with using *Fucus* thalli as substrate, both regarding the behaviour of the omnivore and the grazers, and from scaling macroalgal biomass to the weight of the *Fucus* thallus. (1) Consumers strongly prefer the ephemeral micro- and macroalgae compared to the leathery *Fucus* thallus (Orav-Kotta and Kotta 2004), but when food is scarce consumers may start to feed also on *Fucus* (Hemmi et al. 2004). (2) In grazer-free conditions, strong overgrowth may hamper the growth of *Fucus* or cause degeneration of the tissue. (3) Treatments with strong grazing may promote *Fucus* growth by decreasing competition from epiphytic algae (Råberg and Kautsky 2008). We did not monitor the growth of each *Fucus* individual, but we tested for and found no systematic differences in *Fucus* biomass between treatments at the end of the experiment (no significant differences in dry weight between treatments - data not shown). Since the selection of *Fucus* thallus for the mesocosms were random, this indicates that there was no excessive growth or consumption in any treatment. We found no bite marks on *Fucus*, suggesting direct grazing was minimal (e.g. Hemmi et al. 2004). We also observed no degenerating *Fucus* thallus during the experiment. Furthermore, there was plenty of alternative algal prey during the experiment. No treatment combinations were completely devoid of micro- or macroalgae. We also tested experimental effects on ephemeral macroalgae without scaling for *Fucus* biomass, and this did not affect the results (not shown).



## Results

*Palaemon* had strong effects on the composition of the herbivore community by preying on *Gammarus*, but not *Theodoxus* (Figure 4.2). *Palaemon* suppressed *Gammarus* abundance by 72 and 79% in the both grazer present and *Gammarus* grazer treatments, respectively (Figure 4.2a) (main effect of omnivore presence: $F_{1,12} = 61.87$, $P < 0.001$), but had no effect on *Theodoxus* abundance in any of the grazer treatments (Figure 4.2b) (main effect of *Palaemon* presence: $F_{1,12} = 2.10$, $P = 0.17$). In the absence of *Palaemon*, *Gammarus* abundance increased from initial densities, which depended on the development of new recruits (size < 3 mm), while *Theodoxus* densities remained unchanged. Thus, *Gammarus* populations thrived with high population growth rates, whereas *Theodoxus* populations survived with low rates of recruitment (as expected from their turnover rate). Additionally, numerous alternative prey were present in the mesocosms, consisting of copepods, small gastropods (*Hydrobia* spp.) and isopods (*Idotea* spp.) that either arrived with the water supply or were associated with the *Fucus* thallus (Figure 4.2c). *Palaemon* presence significantly decreased abundances of alternative prey, as the total abundance of alternative

prey was 1.8 times as high in mesocosms without *Palaemon* (numbers without *Palaemon*: 128.5 ± 16.9, numbers with *Palaemon*: 71.2 ± 11.2, average per mesocosm ± SE; Table 4.1, Figure 4.2c).

Grazer presence controlled the development of colony forming diatoms independent of the presence of *Palaemon* (Tables 4.1 and 4.2). In the treatments without grazers, diatoms (mainly of the genus *Melosira*) formed dense floating mats in the mesocosms (Supplement 1), and the biomass was 2.5 times higher compared to the average in treatments with grazers present, both with and without *Palaemon* (Figure 4.3a). Grazer presence also led to a strong decrease in the biomass of attached microalgae (uniseriate green algae: *Punctaria tenuissima* (C. Agardh) Greville, *Mougeotia* spp. and *Ulothrix* spp., and cyanobacteria), which grew both on the sides and bottom of the mesocosm and epiphytic on the *Fucus* (Figure 4.3b, Tables 4.1 and 4.2). Presence of *Theodoxus* (both in the single species and the both grazer present treatments) suppressed the biomass of attached microalgae by half compared to the *Gammarus* treatment (Figure 4.3b, Table 4.2), indicating that *Theodoxus* was a much more effective grazer on attached microalgae than *Gammarus*. There were no significant effects of *Palaemon* on colony forming diatoms or attached microalgae (Table 4.1), indicating that *Palaemon* did not consume microalgae.

The grazer treatments had significant effects on the total biomass of all ephemeral macroalgae (Table 4.1). In contrast to attached microalgae, *Gammarus* presence suppressed the macroalgal biomass by more than half compared to the *Theodoxus* treatment (Figure 4.3c, Table 4.2), indicating strong effects of grazer identity on epiphytic micro- and macroalgae. Although *Gammarus* grazed significantly on macroalgae, in general grazer

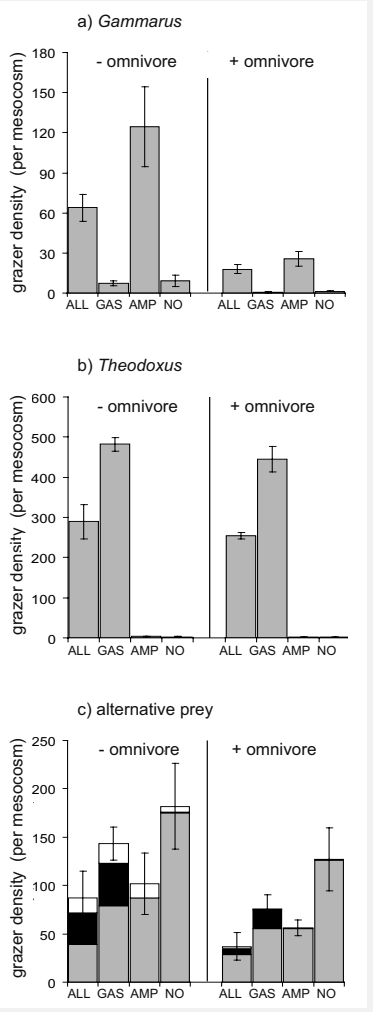


**Figure 4.2** Density of grazers in outdoor mesocosms after 31 days depending on the grazer identity treatment and the presence or absence of the omnivorous shrimp *Palaemon*; **a)** the amphipod *Gammarus*, **b)** the gastropod *Theodoxus* and **c)** alternative prey: grey bars = copepods, black bars = small gastropods, white bars = isopods. Grazer treatments: ALL = adding both *Theodoxus* (250 ind.) and *Gammarus* (25 ind.), GAS = adding *Theodoxus* (500 ind.), AMP = adding *Gammarus* (50 ind.), NO = no grazers added. Means ± SE.

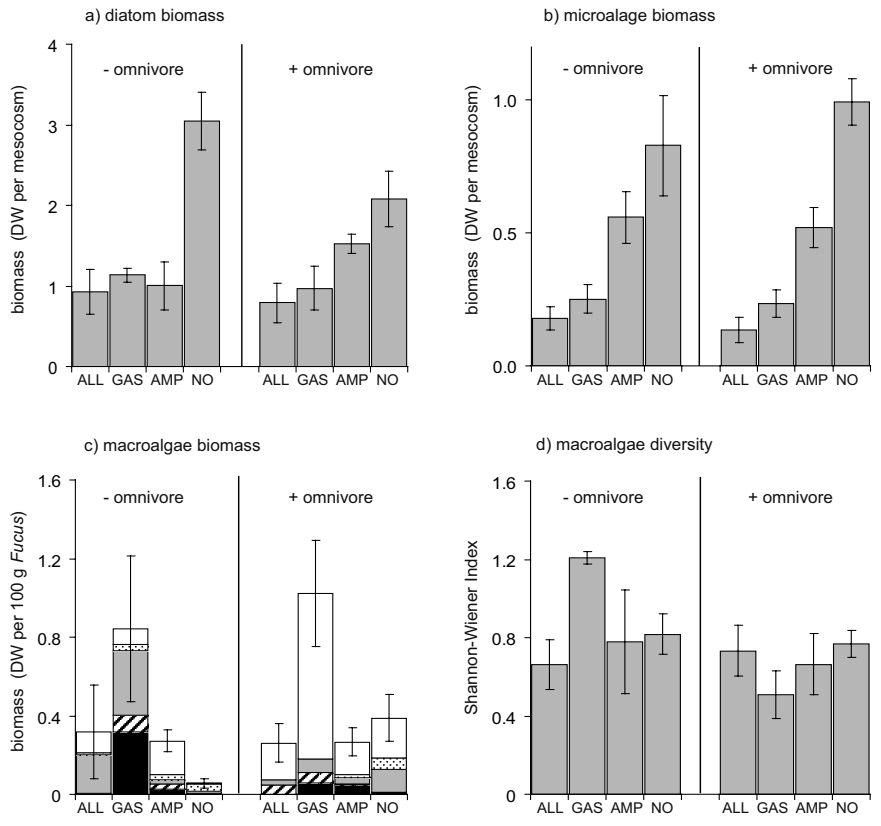


**Figure 4.3** Abundance of algae in outdoor mesocosms after 31 days depending on the grazer treatment and the presence or absence of the omnivorous shrimp *Palaemon*; **a)** biomass of colony forming diatoms in water, **b)** biomass of attached microalgae, **c)** biomass of ephemeral macroalgae: white bars = *Pylaiella littoralis*, dotted bars = Ulva spp., grey bars = *Dictyosiphon foeniculaceus*, striped bars = *Ceramium tenuicorne*, black bars = *Cladophora glomerata*, **d)** species diversity of ephemeral macroalgae.
Grazer treatments: ALL = adding both *Theodoxus* (250 ind.) and *Gammarus* (25 ind.), GAS = adding *Theodoxus* (500 ind.), AMP = adding *Gammarus* (50 ind.), NO = no grazers added. Means ± SE.

presence had a significantly positive effect on macroalgae compared to the no grazer treatments (Table 4.2), probably due to high loads both of colonial and attached filamentous microalgae outcompeting the macroalgae in the absence of grazers. Accordingly, in the treatments without grazers, there was a significant negative correlation between the cover of colonial microalgae and the biomass of the dominating ephemeral macroalgae, *Pylaiella littoralis* (Pearson product moment correlation, r = -0.73, $t_8$ = 2.8, P = 0.026).

There were no significant omnivore (*Palaemon*) effects on the total biomass of ephemeral macroalgae (Figure 4.3c, Table 4.1). However, there was a significant

**Table 4.1** General and generalized linear model results (presented by the F and Wald statistic, respectively) for the abundance of alternative prey (copepods, small gastropods and isopods) and micro- and macroalgae in response to different grazer treatments with and without omnivores.

| | | Alternative prey (number) | | Colony forming diatoms (dw) | | Attached microalgae (dw) | | Ephemeral macroalgae (dw) | | Species diversity (H'): macroalgae | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Source | Df | F | P | F | P | F | P | F | P | Wald | P |
| Omnivore presence (O) | 1 | 9.24 | **0.005** | 1.02 | 0.320 | 0.04 | 0.836 | 2.45 | 0.129 | 4.99 | **0.026** |
| Grazer identity (G) | 3 | 5.68 | **0.004** | 16.10 | **0.000** | 28.44 | **0.000** | 8.88 | **0.000** | 0.19 | 0.911 |
| O x G | 3 | 0.20 | 0.895 | 2.60 | *0.070* | 0.60 | 0.621 | 0.80 | 0.504 | 7.72 | **0.021** |
| Block | 4 | 2.38 | *0.077* | - | - | - | - | 2.59 | *0.059* | 6.91 | 0.141 |
| Error | 28 | | | | | | | | | | |

*If the block factor appeared P < 0.50, it was removed from the statistical model.*

interaction effect between the omnivore and grazer treatments both on the community composition of ephemeral macroalgae (significant MANOVA effect for the interaction between omnivore presence and grazer identity: $F_{10,80} = 3.45$, $P < 0.01$; Figure 4.3c) and macroalgal diversity (expressed as Shannon-Wiener Diversity; Figure 4.3d, Table 4.1). *Palaemon* grazed significantly on green algae, suppressing the biomass of *Cladophora glomerata* and *Ulva* spp. in the *Theodoxus* treatment (Supplements 2 and 3, Table 4.3). *Palaemon* also had a positive effect on *Pylaiella littoralis* in both treatments without *Gammarus*. Presence of *Palaemon* thereby suppressed diversity of ephemeral macroalgae in the *Theodoxus* treatment by increasing the dominance of the brown alga *Pylaiella littoralis* (reducing the evenness of species diversity). Indirect effects of *Palaemon* were restricted to the red algae *Ceramium tenuicorne*, which was positively affected by *Palaemon*, but only when both *Theodoxus* and *Gammarus* were present in the treatment (Supplements 2 and 3,

**Table 4.2** Statistical results and effect sizes ($\acute{\eta}^2$) from planned comparisons of grazer effects within the general linear models describing experimental effects on the biomass of micro- and macroalgae.

| | | Colony forming diatoms | | | Attached microalgae | | | Ephemeral macroalgae | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Effect | Df | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ |
| *Grazer presence* | | | | | | | | | | |
| ALL & GAS & AMP vs NO | 1 | 45.68 | **<0.001** | -0.52 | 58.89 | **<0.001** | -0.50 | 5.30 | **0.029** | +0.08 |
| *Grazer complementarity* | | | | | | | | | | |
| GAS vs AMP | 1 | 0.71 | 0.406 | 0.01 | 13.56 | **0.001** | -0.11 | 12.91 | **0.001** | +0.19 |
| ALL vs GAS & AMP | 1 | 1.92 | 0.176 | 0.02 | 12.87 | **0.001** | -0.26 | 8.43 | **0.007** | -0.13 |
| ALL vs AMP | 1 | 2.63 | 0.115 | 0.03 | 24.48 | **<0.001** | -0.21 | 0.52 | 0.479 | 0.01 |
| ALL vs GAS | 1 | 0.61 | 0.441 | 0.01 | 1.60 | 0.215 | 0.01 | 18.58 | **<0.001** | -0.28 |

*Signs indicate direction of significant grazer effects.*
*Grazer treatments: ALL = adding both* Theodoxus *and* Gammarus, *GAS = adding* Theodoxus, *AMP = adding* Gammarus, *NO = no grazers added.*
*For general GLM results, see Table 4.1.*

Table 4.3). Thus, we found direct negative effects of omnivore grazing on green macroalgae that affected the general diversity of the macroalgal community, and indirect positive effects restricted to one species of red macroalgae.

**Table 4.3** Statistical results and effect sizes ($\acute{\eta}^2$) from planned comparisons of direct and indirect effects of *Palaemon* spp. within the general linear models describing experimental effects on the biomass of individual macroalgal species.

| | | *Ceramium tenuicorne* | | | *Cladophora glomerata* | | | *Dictyoiphon foeniculaceus* | | | *Pyliaella littoralis* | | | *Ulva* spp. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ | F | P | $\acute{\eta}^2$ |
| *Direct consumption:* | | | | | | | | | | | | | | | | |
| NO (No grazer) | 1 | 0.21 | 0.653 | 0.00 | 0.12 | 0.728 | 0.00 | 0.37 | 0.546 | 0.01 | 10.86 | **0.003** | +0.11 | 0.40 | 0.533 | 0.01 |
| GAS (*Theodoxus*) | 1 | 1.58 | 0.220 | 0.02 | 13.67 | **0.001** | -0.17 | 1.88 | 0.182 | 0.05 | 25.95 | **<0.001** | +0.25 | 6.69 | **0.015** | -0.13 |
| *Indirect predation:* | | | | | | | | | | | | | | | | |
| AMP (*Gammarus*) | 1 | 1.55 | 0.223 | 0.02 | 0.19 | 0.670 | 0.00 | 0.24 | 0.630 | 0.01 | 0.57 | 0.458 | 0.01 | 0.38 | 0.545 | 0.01 |
| ALL (both grazers) | 1 | 8.54 | **0.007** | +0.12 | 0.00 | 0.998 | 0.00 | 0.82 | 0.374 | 0.02 | 1.04 | 0.316 | 0.01 | 0.40 | 0.533 | 0.01 |

*Signs indicate the direction of significant omnivore effects.*
*For general GLM results, see Supplement 2.*
*Direct effects = effects of* Palaemon *presence in grazer identity treatments without* Gammarus *(GAS and NO). Indirect effects = effects of* Palaemon *presence in grazer identity treatments with* Gammarus *(AMP and ALL).*

## Discussion

In our experiment, the omnivorous shrimp *Palaemon* had significant direct effects on the composition of both the herbivore and the algal trophic levels by effectively consuming *Gammarus* and ephemeral green macroalgae. *Palaemon* decreased the density of the amphipod *Gammarus* strongly but had no effect on gastropod abundance (*Theodoxus*). In the absence of *Gammarus*, *Palaemon* also had significant effects on macroalgal community composition. By reducing green macroalgae, *Palaemon* did not suppress the total production of ephemeral macroalgae, but strongly promoted the dominance of brown algae (*Pylaiella littoralis*) and concomitantly reduced species diversity. Alternative prey was present in all treatment combinations suggesting that experimental effects were not caused by experimentally induced starving. Thus, we demonstrate that vertical food web effects of an omnivore depend on the functional composition of grazers, where the relative amount of consumption on the grazer and algal trophic levels by *Palaemon* depended on the availability of amphipod prey.

We documented no significant indirect predation effects by *Palaemon* on total primary biomass in the experiment. However, there was a significant positive effect of *Palaemon* presence on the red algae *Ceramium tenuicorne* when both grazers were present, which may have been caused by *Palaemon* predation. Thus, we demonstrated a species cascade from including the omnivorous shrimp on one macroalgal species, but no community-wide trophic cascade on the total biomass of the macroalgal community. *Palaemon* decreased the abundance of *Gammarus* by 80% and *Gammarus*, in turn, decreased the total biomass of ephemeral macroalgae to a third. This indicates potential for a strong reciprocal relationship between these three groups. This is supported by other experiments in which *Palaemon*, through strong predation on *Gammarus locusta* (L), induced trophic cascades that led to an increase in macroalgal biomass up to seven times, when allowed to become the dominant predator (Moksnes et al. 2008, Persson et al. 2008). However, in our experiment, direct grazing effects by *Palaemon* on green macroalgae determined the macroalgae community in the grazer treatment without *Gammarus*. This indicates that *Palaemon* may have suppressed the development of a community-wide trophic cascade by grazing on green macroalgae when the abundance of *Gammarus* decreased (no change in the total biomass of ephemeral macroalgae in the treatments with *Gammarus*). We found no direct grazing effects of *Palaemon* on *C. tenuicorne*, which may explain the significant positive indirect effects of *Palaemon* on this species (significant species cascade). Interestingly, isotope analyses show that *Palaemon* can modify their food preferences, consuming mainly grazers in some areas and mainly ephemeral macroalgae in other areas, perhaps depending on the availability of smaller sizes of mesograzer prey (Jephson et al. 2008, Persson et al. 2008). Thus, our experiment supports the role of omnivory in suppressing trophic cascades when omnivores compensate for their predation effects on herbivores through their ability to graze on primary producers.

In general, herbivores benefit producer evenness in marine systems (Hillebrand 2003, Hillebrand et al. 2007). However, the broad interpretation generally applies to systems with one strong dominant species that is sensitive to grazing (e.g. Altieri et al. 2009), whereas in our study system, grazing instead promoted dominance by one macroalgal species (*P. littoralis*). Dominance determines the distribution of traits in a community, and species evenness may therefore have a stronger effect on community function than species richness (which determines the number of traits) (Hillebrand et al. 2008). In our experiment, there was no relation between species dominance and the accumulation of macroalgal community biomass. However, species evenness of natural macroalgal communities tend to increase production but not necessarily standing biomass (Altieri et al. 2009, Arenas et al. 2009), which indicate that the documented interaction between grazers and macroalgae dominance in our experiment may have significant long-term effects on the function of the community. Like many brown algae, *P. littoralis* exudes toxic substances that may deter herbivores (Råberg et al. 2005), and this may explain the dominance of *P. littoralis* in treatments with a high grazing pressure. Although the omnivore *Palaemon* demonstrated the same complementary grazing function on macroalgal structure as the mesograzer *Gammarus*, *Palaemon* promoted *P. littoralis* dominance even more. This can be seen in the uncontrolled increase in macroalgal biomass in the omnivore treatment without

*Gammarus*, when *P. littoralis* escaped top-down control. Similar positive effects were demonstrated on brown algae by omnivorous benthic fish when the main mesograzer amphipod (*Ampithoe longimana* Smith) was removed (Duffy and Hay 2000). Our results fit simple model predictions stating that a herbivore must exploit the common resource with a higher efficiency than an omnivore to enable coexistence in an omnivorous three-level food web (Polis and Holt 1992, Diehl 1993).

The degree of diet overlap by gastropod and crustacean grazers determined the structure of the algal community. Our study confirms earlier results that grazer identity determines algal community composition and production (Råberg and Kautsky 2007b): the gastropod *Theodoxus* grazed more on microalgae, and the amphipod *Gammarus* controlled macroalgae. There were no significant differences in production of microalgae between the both grazer present and the *Theodoxus* treatment, and no significant differences in production of macroalgae between the both grazer present and the *Gammarus* treatment. This demonstrates the strong species identity effects on grazing rates predicted by theoretical models (Symstad et al. 1998, Loreau and Hector 2001). However, both functional groups of mesograzers were needed to control both the macro- and microalgal production, demonstrating complementarity effects on top-down control in aquatic systems by resource partitioning between grazer groups shown by other studies (Duffy et al. 2003, Råberg and Kautsky 2007b). In absence of both functional groups of mesograzers, a thick layer of colonial microalgae developed on the surface of the mesocosms. This phenomenon is common in sheltered bays in the study area, and our results support that idea that some of the variation in natural algal blooms can be explained by different grazing rates (Eriksson et al. 2009). Moreover, our results indicated a strong trade-off between palatability and the ability to respond to resource fluctuations between the functional groups of mesograzers. For example, *Theodoxus* abundance was constant throughout the experiment, and we detected no significant predation effects by the omnivore and no new recruitment into the mesocosms. *Gammarus*, on the other hand, was heavily decimated by omnivore predation, but also showed a strong recruitment of new individuals into the mesocosms. Thus, *Theodoxus* is a 'static grazer' with little capacity to quickly change population size in response to favourable changes in the environment, but at the same time comparably resistant to predation. *Gammarus*, on the other hand, is more a 'dynamic' grazer with the capacity to quickly change population size, but was comparably sensitive to predation.

Our experiment demonstrates two properties of food webs that prevent community level trophic cascades: (1) strong direct effects by omnivores on more than one trophic levels and (2) a diversified prey community where at least one dominant grazer is tolerant to predation. The ability to feed on alternative prey makes omnivores less dependent on fluctuations in single prey populations, which promote persistence and may intensify top-down control (Polis and Strong 1996, Eubanks and Denno 1999). In some systems, strong top-down control by omnivores also translates to strong trophic cascades on plant or algal biomass, e.g. as demonstrated in salt marsh and seagrass ecosystems (Ho and Pennings 2008, Moksnes et al. 2008). In both the salt marsh and seagrass example, the omnivore induced a trophic cascade because it fed selectively on the main herbivore rather than

plants or algae when both where available (Ho and Pennings 2008, Moksnes et al. 2008). Moreover, both studies also present species cascades involving one major herbivore on one plant or algal species only. In our system, functional complementarity at both the grazer (amphipods and gastropods) and algal (micro-/macroalgae) trophic levels compensated for decreases in the other group. Only when both grazer groups were removed from the system, the total biomass of micro- and macroalgae together increased. Thus, while species cascades may be common in food webs, community level trophic cascades are probably rare in natural communities due to omnivory and within trophic level trait diversity (Polis 1999).

The linking of reduction in top-predators to massive increases of mesopredator populations is common in exploited ecosystems (Eriksson et al. 2009, Ritchie and Johnson 2009). The impact of mesopredator-release events depends on food web connectivity, where a high number of weak trophic links should decrease the strength of top-down control and reduce the probability of trophic cascades (Dunne et al. 2002, Neutel et al. 2002, Duffy et al.2007). Our results show that even though omnivores have links to more than one trophic level, the links may be strong and switch in magnitude depending on availability and functional composition of the prey community. For example, Moksnes et al. (2008) suggested that increases in *P. elegans* from large scale decreases in apex predators (*Gadhus morhua* L, cod) have suppressed mesograzers abundances (mainly amphipods) and thereby indirectly contributed to increases in macroalgal production in the coastal zone of the Skagerrak (North Sea). In our study area (the Baltic Sea), substantial mesopredator release events of small-bodied fish have reduced grazing rates, and thereby dramatically increased local biomass production of ephemeral micro- and macroalgae (Eriksson et al. 2009, Sieben et al. 2011b). However, the results of the present study suggested that the main impact caused by the presence of *Palaemon* was a decrease in macroalgal diversity, because *Palaemon* was able to include filamentous algae in its diet when palatable grazers decrease. Thus, to predict effects of changing abundances of omnivores, we need to acknowledge that omnivores may have deep vertical effects in food webs by links to several trophic levels. This specifically calls for incorporating properties of the food web, which determine the dynamics between indirect and direct effects of omnivores, such as interactions between the functional diversity on adjacent trophic levels and palatability of prey populations.



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# A mesopredator release of stickleback promotes recruitment of macroalgae in the Baltic Sea

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**Abstract**

In the Baltic Sea, increased populations of the three-spined stickleback are invading the coastal zone in summer, following declines in large predatory fish such as cod, pike, and perch. Here, we explore the consequences of such a meso-predator release on a near-natural scale, by manipulating stickleback densities in four large 600 $m^2$ enclosures: two 'removal' and two 'addition' enclosures. Higher densities of stickleback resulted in a three times higher recruitment of ephemeral green macroalgae. At the same time we found higher abundances of the dominating invertebrate grazers with lower stickleback densities: higher numbers of both amphipods and smaller gastropods were found in one stickleback 'removal' enclosure and higher numbers of large gastropods occurred in the other 'removal' enclosure. Grazer abundances also depended on the macrophyte species that dominated the enclosures. Nutrient enrichment had no statistically significant effect on algal recruitment, although the mean number of algal recruits was almost doubled under enriched conditions. Our results indicate that a meso-predator release of stickleback may dramatically shift coastal food web constitution towards increased abundances of ephemeral macroalgae through a trophic cascade.

## Introduction

Anthropogenic impacts have changed the structure of aquatic ecosystems on a global scale (Lotze et al. 2006, Worm et al. 2006). Overexploitation of particularly large-sized fishes has caused declines in top-predator populations, which often is associated with increases in abundance of medium-sized predators (Heithaus et al. 2008, Myers et al. 2007). Such meso-predator release events (Ritchie and Johnson 2009) in turn can have reciprocal cascading effects on lower trophic levels of herbivores and producers. Trophic cascades have been demonstrated in lakes (Carpenter et al. 1985), streams (Power 1990), kelp forests (Estes et al. 1998), estuaries (Jackson et al. 2001), rocky intertidal systems (Menge 2000), continental shelves (Frank et al. 2007) and also in the open ocean (Ward and Myers 2005). Recent studies provide strong indications that fisheries-induced declines in top-predators have increased the occurrence of algal blooms (Casiniet al. 2008, Daskalov et al. 2007) and gelatinous plankton (Vasas et al. 2007) through cascading trophic interactions. System productivity appears to be a key factor to strengthen or suppress trophic cascades (Polis 1999). Accordingly, nutrient enrichment may promote the propagation of trophic cascades from top-predatory fish to algae (Eriksson et al. 2009, Sieben et al. 2011, Vasas et al. 2007).

Coastal eutrophication management programmes usually aim to combat eutrophication symptoms by controlling the nutrient input only, whereas the role of biological communities for regulating ecosystem functioning has only been incorporated in lake management (Søndergaard et al. 2007). In order to evaluate potential synergistic effects of fisheries exploitation and coastal eutrophication, large-scale food web studies are strongly needed. Ecological experiments on an ecosystem-relevant scale are a compromise of dealing with high natural variability (large scale but heterogeneous environment) and a limited capability of extrapolating the experimental results (homogeneous environment but small scale). However, whole-lake experiments show that the release of piscivores in formerly planktivore-dominated lakes can substantially reduce producer biomass (Carpenter et al. 2001) and therefore control nuisance phytoplankton blooms. Hence, biomanipulation has become a powerful tool to limit primary production in eutrophied lakes, mainly through the removal of zooplanktivorous or benthivorous fishes (e.g. Søndergaard et al. 2007). Here, we present a study that explores consequences of a meso-predator release in a marine coastal food web on a near-natural spatial scale.

In the Swedish part of the Baltic Sea, a dramatic increase in a meso-predator fish, the three-spined stickleback (*Gasterosteus aculeatus aculeatus* L) has taken place during the last decade (Ljunggren et al. 2010). At the same time the population of the major piscivore in the Baltic Sea, cod (*Gadus morhua* L), has been very low (ICES 2009), as have been the populations of pike (*Esox lucius* L) and perch (*Perca fluviatilis* L) in some coastal areas (Lehtonen et al. 2009, Ljunggren et al. 2010, Nilsson et al. 2004). Stickleback is a species that spends most of its life-cycle offshore and migrates to shallow coastal areas in the spawning period. From 2003 to 2007, offshore abundances of stickleback increased by 20 times, and today, it is the most abundant fish in shallow bays along some stretches of the Swedish coast of the Baltic Sea in summer (Eriksson et

al. 2009, Ljunggren et al. 2010). In stickleback-dominated bays, the abundances of perch and pike are lower and the occurrence of filamentous algal blooms is up to 5 times higher than in areas where perch and pike are common, indicating a relation between predator declines and filamentous algal blooms inthe Baltic Sea (Eriksson et al. 2009, Ljunggren et al. 2010). Accordingly, small-scale experiments demonstrated that excluding perch and pike increased stickleback abundances, and thereby promoted the recruitment of filamentous algae by negative effects on invertebrate grazers (Eriksson et al. 2009, Sieben et al. 2011).

Here, we expand the scale of these experiments to large field enclosures, to explore effects of the temporary meso-predator invasion by stickleback on the coastal system. We hypothesise, that local invasions of stickleback 1) change the composition of invertebrate grazer communities, thereby 2) induce a trophic cascade on the recruitment of ephemeral algae, which 3) interacts with nutrient enrichment. This is one of the first empirical tests of large-scale release effects of a marine meso-predator on two lower trophic levels.

## Methods

### Study site and organisms

The experiment was performed in a shallow bay in the Swedish archipelago at Ödängla, Mönsterås, southern Baltic Proper, in summer 2008. The site is sheltered and non-tidal. Salinity is around 7 PSU in summer. The mainly soft bottom is scattered with sand and boulders and is in the shallowest part (< 0.5 m) replaced by rock. Proliferous submerged vegetation provides an important habitat for diverse invertebrates and epiphytes (Wikström and Kautsky 2004). In the study area, the submerged vegetation is dominated by the watermilfoil *Myriophyllum spicatum* L and the pondweed *Stuckenia* (formerly: *Potamogeton*) *pectinatus* (L) Börner and in the upper sublittoral (< 1 m depth) also by the brown seaweed *Fucus vesiculosus* L. The invertebrate grazers are dominated by gastropods (*Hydrobia* spp., *Theodoxus fluviatilis* L, *Radix balthica* (L), *Potamopyrgus antipodarum* (JE Gray) and *Bithynia tentaculata* (L), hereafter *Hydrobia*, *Theodoxus*, *Radix*, *Potamopyrgus* and *Bithynia*) and amphipods (mainly *Gammarus* spp., hereafter *Gammarus*). The gastropod species are efficient consumers of diatoms, microalgae and propagules of macroalgae (Kofoed 1975, Korpinen et al. 2008). *Gammarus* species are considered selective omnivores, feeding on adult macroalgae as well as their propagules, larger plant material, fine detritus, other invertebrates and fish eggs (Lotze and Worm 2000, MacNeil et al. 1999, Orav-Kotta and Kotta 2003). The fish community is mainly composed of freshwater species, but also marine species occur. Common fish species are three-spined stickleback (*G. aculeatus aculeatus* L), bleak (*Alburnus alburnus* (L)), rudd (*Scardinius erythrophthalmus* (L)), White bream (*Blicca bjoerkna* (L)), roach (*Rutilus rutilus* (L)), European perch (*P. fluviatilis* L) and Northern pike (*E. lucius* L). In 1995–2008, declining numbers of pike, ruffe and roach have been observed in the area, through local monitoring programmes, while white bream, ide, bleak and rudd increased

(Swedish Board of Fisheries Monitoring Programme). Catches of perch have been low throughout this period. Smaller fishes like stickleback were not covered by these surveys. A first survey on small-bodied fish in spring and early summer 2009 showed that stickleback represented more than 90% of the total fish abundances (May and June: 94% and90%, respectively) and more than 28% of the total biomass (May and June: 28% and 31%, respectively) (Swedish Board of Fisheries Monitoring Programme).

## Experimental design

We tested large-scale effects of a meso-predator release on the adjacent trophic levels, invertebrate grazer and algae assemblages, by manipulating stickleback abundances in enclosures. In order to approach an ecosystem-relevant scale, we set up four large enclosures of approximately 20 × 30 m (600 $m^2$) by closing off beach sections with nets. The low number of replication was a compromise of obtaining a low variability both within and between cages, and of having enclosures that are large enough to capture the mass effects of stickleback invasions. Larger cages are likely to decrease the between-cage variability but also to increase the within-cage variability due to environmental heterogeneity (e.g. vegetation, depth and sediment). Therefore, all four cages were placed in the same bay along the shoreline with a gap of 5 m between neighbouring cages. The resulting depth gradient within each enclosure ranged from 0 to 1.5 m. Wooden pillars were used as construction for nylon netting (mesh size: 6 mm) that built the enclosures. Lead was attached to the bottom end of the nets and kept them vertically in the water column. Net height was individually adjusted to the water depth and checked during snorkelling observations to make sure that they reached the bottom. We removed fish from every second enclosure by beach seining (two times per enclosure; = 'stickleback removals' R1 and R2). Sticklebacks caught with the seine net (several 1000) were used to fill the other two enclosures (= 'stickleback additions' A1 and A2). Secondly, small underwater detonations (see Snickars et al. 2007), covering the deeper parts, were used in these enclosures to further decrease densities of stickleback from the 'stickleback removals'. Finally, minnow traps (mesh size 5 mm) were put up inside the deep end of the 'stickleback removals' at a depth of 1 m to continuously keep the cages clear of sticklebacks. The traps were checked and fishes were removed every day. The experiment started by removing the fishes on 13 June 2008 and ran until 23 July 2008.

The combined effect of a meso-predator release and nutrient enrichment on algal abundance was tested by supplying nutrients to algal substrates (bricks) placed in the enclosures. Four bricks were placed at 1 m depth in each enclosure, at least 3 m apart to avoid spill-over from the nutrient treatments. This distance has been shown as sufficient to avoid cross-fertilisation (Worm et al. 2000). The minimum distance of the bricks from the enclosure net was 1 m. The fertiliser was supplied by attaching elongated mesh bags (20×10 cm, mesh size: 1 mm) filled with 120 g coated slow-release N–P–K fertiliser pellets (Plantacote Depot 6 M, Urania Agrochem, Hamburg, Germany) to half of the bricks in each enclosure. Nutrient treatments (ambient or enriched) were randomly assigned within each enclosure. The pellets continuously enrich the water

column with nitrogen (14%, as $NH_4$–N and $NH_3$–N), phosphorus (9%, as $P_2O_5$) and potassium (15%, as $K_2O$). This method has been validated to enrich the water column (Worm et al. 2000) and commonly increase net biomass production by more than two times (Eriksson et al. 2009).

## Sampling

Sticklebacks occur predominantly in habitats of 90–120 cm depth, which is also their preferred feeding depth (Thorman and Wiederholm 1986). Therefore, all samples of invertebrates and algae were taken in a transect parallel to the shoreline at about 1 m depth to avoid cross-effects with water depth. In order to estimate stickleback densities in the experimental plots we used minnow traps of the same kind as described above (9 traps per plot), but now they were placed in the same transects where invertebrate and algae samples were derived from. Fishes were counted on 18 and 19 June, as well as on 23 and 24 July, 24 h after placing the traps. The invertebrate communities were sampled by collecting the macrophyte that they were associated with. The associated fauna is related to the macrophyte biomass and differs among macrophyte species (Wikström and Kautsky 2004). Hence, in order to obtain a general picture of the invertebrate community, we sampled the three dominating species *Fucus vesiculosus*, *Myriophyllum spicatum* and *Stuckenia pectinatus* (hereafter *Fucus*, *Myriophyllum* and *Stuckenia*). The sampled plants *Myriophyllum* and *Stuckenia* were on average 50 cm high, *Fucus* height was on average 30 cm. A fine net bag (mesh size: 1 mm) was pulled over three randomly selected individuals of each of the three macrophytes species in each enclosure (N = 3) resulting in 9 macrophyte samples per enclosure, enclosing all of the associated fauna underwater. Samples were stored in cooling boxes, before being transported to the lab, where they were deep-frozen. Invertebrates were sampled twice, on 19 June and on 23 July. Only the samples from June were included in the analyses because sticklebacks vanished from the area already in early/mid-July (see results of fish counting). Sampling in June took place only one week after the set-up of the experiment, but stickleback density was very high at this time and meso-predator effects on the mobile grazer fauna should have developed rapidly. Animals were sorted under a dissecting microscope, determined to the species level if possible and counted. Macroalgal recruitment was sampled on unglazed ceramic tiles (5 cm × 5 cm). Two tiles were glued on top of each of the algal substrates (bricks). We used the number of recruits over biomass since top-down control of algae is strongest at early life-stages (Lotze and Worm 2000). Macroalgal tiles were sampled on 23 July. The number of recruits on each tile was counted under a dissecting microscope. The counts were pooled for each macroalgal substrate (two tiles), resulting in two replicates of recruit abundances per nutrient level (N = 2) in each enclosure. Sticklebacks equally prefer feeding above vegetated and stony substrates, where their diet contains more types of food, than above sandy substrates (Ibrahim and Huntingford 1989). The algal substrates were placed in gaps (ca. 0.25 $m^2$) in the vegetation among naturally occurring small boulders and rock. We therefore

assumed that predation from stickleback on invertebrates grazing on the tiles was similar to predation on invertebrates associated with macroalgae or plants.

### Statistical analyses

Differences in algal recruits and invertebrates were tested by analyses of variance (ANOVAs). The effects of the stickleback treatment (see fish counts below) as well as the environmental conditions (spatial differences in macrophyte distribution) differed between enclosures. Thus, we abandoned the 'addition' vs. 'removal' treatment and used four levels (Addition 1, Addition 2, Removal 1 and Removal 2) as a fixed factor instead in the analyses. Macrophyte biomass did not relate significantly to the invertebrate numbers, but the macrophyte species had a very large effect. Macrophyte species was therefore included as a second fixed factor in the ANOVAs for invertebrate abundances. For changes in algal recruits, nutrient enrichment was included as a second fixed factor in the analyses. Grazer and algal recruit counts were square-root transformed if necessary to attain homoscedasticity. Tukey's HSD post-hoc testing was used to analyse enclosure- and macrophyte species-specific differences. Fish counts were first tested with the simplest model, a one-way ANOVA using the two treatment levels 'addition' and 'removal'. In order to attain consistency within the analyses, we also included the ANOVA results on the four treatment levels (Addition 1, Addition 2, Removal 1 and Removal 2) similar to the grazers and algal recruits. Fish counts were also square-root transformed to attain homogeneous variances.



## Results

Stickleback densities were reduced in the removal enclosures compared to the addition enclosures (4-level ANOVA testing the difference between the four different enclosures: $F_{3,16}$ = 3.18,P = 0.053; 2-level ANOVA testing the difference between addition and removal treatments: $F_{1,18}$ = 5.53, P = 0.03). However, there was still a substantial amount of stickleback left in the removal enclosures, and there was a considerable variation in numbers between the two addition enclosures. In the stickleback removal enclosures were on average 5.6 (R1) and 6.1 (R2) sticklebacks in the traps (per trap per day), which was lower than 10.5 (A1) and 19.4 (A2) sticklebacks in the addition enclosures. In July the stickleback densities dropped to 5–15% of the densities in June (average numbers: 2 and 1.6 in addition enclosures (A1and A2) and 0.3 and 0.5 in removal enclosures (R1 and R2), sticklebacks per trap per day, respectively), probably due to post-spawning mortality. In the stickleback addition treatment, the number of algal recruits was more than three times higher than in the stickleback removal treatments (Figure 5.1, main effect: $F_{3,8}$ = 5.49, P < 0.05). Nutrient enrichment resulted in almost a doubling in the mean number of algal recruits (482 ± 161.3 and 840 ± 312.7, number per $dm^2$, ambient and enriched, respectively, mean ± SE, no interaction effect), but variability of algal abundances was too high to proof statistical significance of the nutrient treatment. The

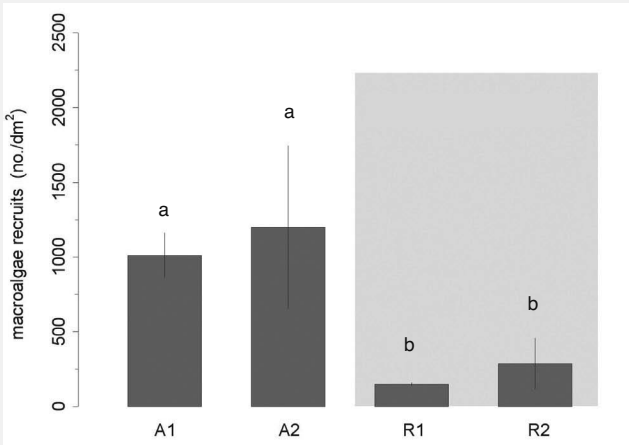


**Figure 5.1** Macroalgae recruit densities (number/dm$^2$) in stickleback addition (A1 and A2) and removal enclosures (R1 and R2). a and b denote significant differences $P < 0.05$ (means ± SE, $N = 2$). The grey area indicates enclosures where stickleback was removed (R1 and R2).

algal recruits consisted mainly of the ephemeral green macroalgae *Cladophora glomerata* (L) Kützing and some *Ulva* spp.

Higher densities of stickleback did not have uniform effects on grazers, but instead we found enclosure-specific changes. The amphipod *Gammarus* was found in highest abundances in one stickleback removal enclosure (R1, Figure 5.2a, Tables 5.1 and 5.2) and mostly on *Fucus* (Figure 5.2a). Abundances of small gastropods (< 3 mm), including *Hydrobia*, *Potamopyrgus*, and small individuals of *Radix*, *Theodoxus* and *Bithynia*, were higher in the same stickleback removal enclosure (R1, Figure 5.2b, Tables 5.1 and 5.2). The increase was mainly due to *Hydrobia*, whereas macrophyte species had no overall effect (Table 5.1). In the other stickleback removal enclosure (R2) the number of large gastropods, i.e. large individuals of *Radix*, *Theodoxus* and *Bithynia*, were greatest on *Fucus*, while abundances were generally low on *Myriophyllum* and *Stuckenia* generating a significant interaction effect between plant host and enclosure (Figure 5.2c, Tables 5.1 and 5.2). The strongest differences of grazer preferences for the macrophyte host species were found between *Fucus* and the two plant species. Thus, higher stickleback densities increased the number of macroalgal recruits strongly in both addition enclosures compared to the removals, while the abundance of amphipods and small gastropods, mainly *Hydrobia*, was highest in one of the removal enclosures (R1), and large gastropods were most abundant in the other removal enclosure (R2).

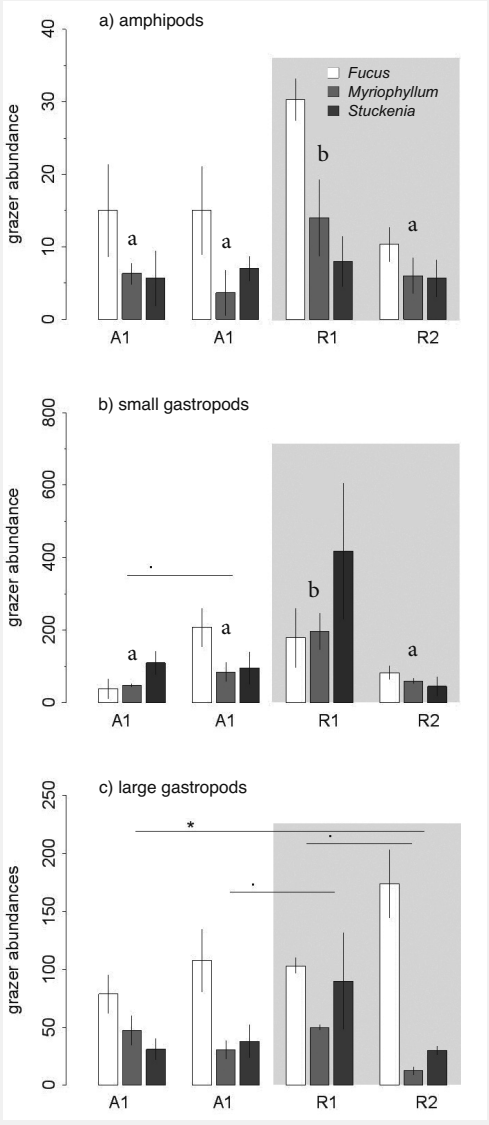


**Figure 5.2** Grazer abundances as number of individuals, **a)** amphipods, **b)** small gastropods, and **c)** large gastropods, in stickleback addition (A1 and A2) and removal enclosures (R1 and R2) on three different macrophyte species: *Fucus* (white), *Myriophyllum* (light grey), and *Stuckenia* (dark grey). a and b denote significant main effects with $P < 0.05$ (means ± SE, N = 3), between enclosures, * and · denote significant post-hoc effects ($P < 0.05$) and marginal trends ($P < 0.1$), respectively. The grey area indicates enclosures where stickleback was removed (R1 and R2).

## Discussion

In this experiment we successfully mimicked meso-predator release effects on an ecosystem-relevant scale in a marine system. In linewith hypotheses 1 and 2, higher abundances of amphipods and gastropods were found with low densities of stickleback, and high densities of stickleback strongly promoted algae recruitment, suggesting reciprocal cascading top-down effects from stickleback. However, the composition of grazer assemblages was highly variable, maybe due to environmental heterogeneity, i.e. differences in the distribution of habitat forming flowering plants or algae between the large cages. In contrast to hypothesis 3, nutrient enrichment had no statistically significant effect on algal recruitment, although the mean number of algal recruits was higher under enriched conditions. Our results support that a meso-predator release of stickleback cascaded down the food web to change the configuration of lower trophic levels in the coastal zone of the western Baltic Sea.

Sticklebacks prefer a planktivore diet (Ibrahim and Huntingford 1989), but when they migrate into shallow areas during the reproductive months, they also feed on e.g. gammarid amphipods (Sieben et al. 2011) and insect larvae (Hynes 1950). It is therefore likely that the lower amphipod abundance in one removal enclosure was a direct

result of stickleback consumption. In contrast, it has not been shown that sticklebacks consume considerable amounts of gastropods. In the course of the stickleback removal also other fish species, which might be potential predators for gastropods, have been removed from the cages. However, only a few other fishes were caught together with several thousand sticklebacks from the removal enclosures, and we assume that predator effects other than from stickleback only played a minor role. Predator effects in general maybe direct through consumption but also indirect through trait-mediated interactions (TMII). TMII refer to non-lethal predator-induced changes in prey behaviour (e.g. in foraging activity), and could ultimately suppress grazing without changing the abundance of the intermediate species. Their contribution to net predator-effects is likely to be underestimated although separating trait-mediated from density-mediated effects is difficult because they are often confounded (Werner and Peacor 2003). Thus, the strong increase of algal recruits and the decrease in gastropod abundances in both cages with high stickleback densities indicate that also non-lethal effects may have been important during the experiment.

Nutrient enrichment did not significantly increase algal recruitment in our experiment, in contrast to our hypothesis and earlier studies (Eriksson et al. 2009, Lotze et al. 2000). However, the abundance of recruitment stages of macroalgae is more often

**Table 5.1** ANOVA results on differences in grazer abundances depending on enclosures with different densities of stickleback and on the identity of sampled host macrophyte species.

| Response variable | Df | F-value | P-value |
|---|---|---|---|
| **Amphipods** | | | |
| Enclosure | 3 | 4.39 | **0.013** |
| Macrophyte | 2 | 10.34 | **<0.001** |
| Enclosure × Macrophyte | 6 | 1.14 | 0.370 |
| Residuals | 24 | | |
| **Gastropods - small** | | | |
| Enclosure | 3 | 6.98 | **0.002** |
| Macrophyte | 2 | 0.57 | 0.574 |
| Enclosure × Macrophyte | 6 | 1.47 | 0.230 |
| Residuals | 24 | | |
| **Gastropods - large** | | | |
| Enclosure | 3 | 1.38 | 0.274 |
| Macrophyte | 2 | 21.60 | **<0.001** |
| Enclosure × Macrophyte | 6 | 2.68 | **0.039** |
| Residuals | 24 | | |

*Bold numbers denote P < 0.05.*

**Table 5.2** Tukey's HSD-Post-hoc-test results of grazer abundances in stickleback addition (A1 and A2) and removal (R1 and R2) enclosures.

| | A1 | A2 | R1 |
|---|---|---|---|
| | stickleback addition | | removal |
| **Amphipods** | | | |
| A2 | 0.888 | | |
| R1 | **0.012** | **0.009** | |
| R2 | 0.599 | 0.699 | **0.004** |
| **Gastropods - small** | | | |
| A2 | *0.098* | | |
| R1 | **<0.001** | **0.034** | |
| R2 | 0.964 | 0.107 | **<0.001** |
| **Gastropods - large** | | | |
| A2 | 0.38 | | |
| R1 | 0.392 | 0.982 | |
| R2 | **0.012** | 0.081 | *0.077* |

*Bold numbers denote P < 0.05, italic numbers denote P < 0.1.*

controlled by consumers than by resources, while the production of biomass normally responds strongly to nutrient enrichment (Erikssonet al. 2009, Lotze and Worm 2000, Lotze et al. 2000). In addition, the nutrient treatment may have been weakened by already high background nutrient loads at the site (http://www.smed.se/) and/or high nutrient levels through nutrient excretion by stickleback. Zimmer et al. (2006) assessed the importance of nutrient excretion by fish to enhance algal production in wetlands and several studies have shown that nutrient recycling by fish can promote phytoplankton production in lakes (e.g. Vanni and Layne 1997, Vanni et al. 1997). The amount of phosphorous transported to the experimental site by stickleback is similar to the estimated load from land-run-off (ca. 100 kg, pers. obs.). However, it is unlikely that the nutrient excretion by stickleback affected the results of the fish treatment by local enrichment in the fish addition enclosures. Very high densities of stickleback in the whole bay suggest strong nutrient enrichment effects in the whole area. This is supported by the fact that there was no effect of the nutrient treatment in the stickleback removal enclosures, and that there was no trend towards interaction between the nutrient and fish treatments.

Furthermore, environmental heterogeneity is an important confounding factor when evaluating trophic interactions on a large scale. Grazer assemblages in this study were affected not only by the experimental treatments but also by differences in the spatial distribution of macrophytes within and between enclosures. One removal enclosure (R2) was on average shallower and strongly *Myriophyllum*-dominated compared to all other enclosures (see Supplementary material), which may have contributed to the overall variation in the grazer assemblages and to the differences in treatment effects between the two stickleback removal enclosures. For future manipulative large-scale experiments we would therefore recommend either to use an environment that is adequately homogeneous over the entire scale of the experiment with respect to parameters that influence the dependent variables (e.g. depth and vegetation), or to replicate the experimental treatment at several sites in a gradient of nutrient loads and/or predator densities. Such approaches, referred to as "pseudo-experimental" (Baum and Worm 2009), could help to disentangle trophic effects from natural noise on ecosystem-relevant scales. The experimental area was prior to this study considered as relatively homogenous, but it turned out that vegetation heterogeneity still had a great impact on grazer assemblages, causing high 'natural variation' beside the treatment effects.

It is widely acknowledged that trophic cascades only occur under appropriate conditions, determined by extrinsic, such as the nutrient status and intrinsic factors, such as certain consumer traits (Polis 1999). Moreover, ecosystems should not be regarded as closed systems. Incorporating spatial dynamics and spatial coupling into food web studies is one attempt to approach the conditions of an open system. Such spatial subsidies are allochthonous inputs, which can enter the food web at different levels: nutrients, primary producers, primary consumers or predators. Subsidised trophic interactions maybe stronger (Polis et al. 1997), and Polis (1999) also hypothesised that subsidies could even act as a prerequisite for a trophic cascade. Furthermore, the productivity of the recipient system plays a key role and thus, nutrient run-off is likely to increase the effect magnitude of atrophic cascade (Elmhagen and Rushton 2007).

Similarly, migrating fish populations could constitute another spatial subsidy. The three-spined stickleback could be a consumer subsidy by feeding in open sea areas and carrying the energy to the coastal zone where they reproduce and thereafter die. Therefore, the seasonal migration of stickleback could drastically change the trophic control of a system that, at the same time, experiences a decline in piscivorous fish. The potential importance of this mechanism is underscored by model predictions showing that inputs at predator or producer levels may result in larger cascading effects than inputs at other trophic levels (Leroux and Loreau 2008). Furthermore, meta-analyses have shown that cross-habitat subsidies have the strongest effects in coastal habitats and cobble bars, probably due to a high perimeter:area relationship, which suggests that coastal zones are likely to be very sensitive for changes in trophic relations (Marczak et al. 2007) because of their relatively large catchment area for such subsidies.

Recent studies emphasise the importance of joint effects of the nutrient status and the functioning of higher trophic levels in affecting harmful algal blooms (Casini et al. 2008, Eriksson et al. 2009). Restoration programmes are therefore strongly needed to prevent ecosystem degradation and collapse, but studies on an ecosystem-relevant scale are scarce and our understanding of the coastal system is still poor. The present study is a first attempt to qualify and quantify large-scale effects of food web changes. We found that an increase in the meso-predatory stickleback positively affected the recruitment of macroalgae, most likely by changing the herbivore community composition.

## Acknowledgments



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# Effects of altered offshore food webs on coastal ecosystems emphasize the need for cross-ecosystem management

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## Abstract

By mainly targeting larger predatory fish, commercial fisheries have indirectly promoted rapid increases in densities of their prey; smaller predatory fish like sprat, stickleback and gobies. This process, known as mesopredator release, has effectively transformed many marine offshore basins into mesopredator-dominated ecosystems. In this article, we discuss recent indications of trophic cascades on the Atlantic and Baltic coasts of Sweden, where increased abundances of mesopredatory fish are linked to increased nearshore production and biomass of ephemeral algae. Based on synthesis of monitoring data, we suggest that offshore exploitation of larger predatory fish has contributed to the increase in mesopredator fish also along the coasts, with indirect negative effects on important benthic habitats and coastal water quality. The results emphasize the need to rebuild offshore and coastal populations of larger predatory fish to levels where they regain their control over lower trophic levels and important links between offshore and coastal systems are restored.

## Introduction

Fishery induced declines in populations of larger predatory fish have generated dramatic changes in the food web composition in offshore and coastal seas (Pauly et al. 1998, Lotze et al. 2006). In particular, decreased stocks of predatory fish have generated strong increases in their prey, medium-sized or "meso-" predators (i.e. "mesopredator release"), changing the interactions between higher trophic levels considerably (e.g. Myers et al. 2007, Baum and Worm 2009). In some instances, there are documented cascading effects from such mesopredator increases on lower levels in the pelagic food web, including community-wide decreases of zooplankton, and increases in jellyfish and phytoplankton (e.g. Frank et al. 2005, Daskalov et al. 2007, Casini et al. 2008).

Effects of overfishing have traditionally been synonymous with effects on commercially important stocks, and on the consequences for either the market actors or coastal human societies that have experienced dramatic changes in their livelihood. There has also been a strong concern for many of the larger pelagic species, which have a high societal impact and cultural value. Management actions have therefore been centred on protecting the economic viability of commercial stocks and on restoring biological diversity of apex predators, such as whales, dolphins, seals, sharks and tuna. Today, most management organizations promote ecosystem-based management (EBM). EBM is an adaptive management approach that focuses on the complexity of interactions within and between ecological and social systems, acknowledging that diversity of species and their traits are important for ecosystem performance and stability (Christensen et al. 1996). For coastal societies, EBM is a favourable long-term strategy because it considers multiple ecosystem services and manage the capacity of ecosystems to tolerate disturbances and stress, rather than focusing on one interest group by managing a single function or the production of one species (Christensen et al. 1996, Leslie and McLeod 2007).

Ecosystems are connected by flows of energy, materials and organisms. Spatial subsidies across ecosystem borders are important for population dynamics and community structure in many recipient ecosystems (Polis and Strong 1996). An important vector that transports resources between offshore and coastal ecosystems is constituted by migrating animals that utilize both systems during their life cycles (e.g. Varpe et al. 2005). The existence of such migrations implies that changes in offshore food webs may profoundly impact coastal ecosystems. For example, in the early 1990s, negative effects of increased predation from offshore populations of killer whales (*Orcinus orca* (L)) were reported from the coast of Alaska (Estes et al. 1998). Killer whales increased their foraging along the coast and thereby limited the coastal populations of sea otters (*Enhydra lutris* (L)). This released the main prey of sea otters - herbivorous sea urchins - from predation control, resulting in severe overgrazing of giant kelp; the habitat-founding species in the ecosystem. There is an increasing realization that major changes in offshore pelagic food webs might impact the functioning of coastal ecosystems, including a reduced production of the crucial ecosystem services they provide.

In this study, we suggest that observed effects of coastal mesopredators on lower trophic levels may in fact be triggered by fishery-induced changes in offshore food webs. We base this hypothesis on analyses of fish monitoring data from two different areas: the

marine Atlantic west coast of Sweden and the brackish Baltic east coast of Sweden, combined with published information on concomitant food web changes, highlighting how changes in offshore food web composition appear to give rise to complex responses also in the coastal ecosystems.

## Increase of mesopredators on the Swedish Atlantic coast

Declines in offshore predator populations may increase the abundance of nearshore mesopredators by direct decreases in predation rates, but also by complex, indirect food web interactions. On the Atlantic coast of Sweden (Skagerrak and Kattegat) the coastal mesopredator community is dominated by wrasses, gobiids and the common shore crab (*Carcinus maenas* (L)) (Pihl and Wennhage 2002, Pihl et al. 2006, Swedish Board of Fisheries unpublished). Long-term monitoring data from a coastal area in the southern basin, Kattegat (Swedish Board of Fisheries, Vendelsö), suggests that these important mesopredators have all become increasingly abundant.

Vendelsö (latitude 57°18', longitude 12°70') is a reference area for the nuclear power plant of Ringhals. The discharge of heated cooling water from the power plant is not expected to affect the Vendelsö area (Bergström et al. 2009). In 1976, a standardized fyke net monitoring programme was initiated in Vendelsö (HELCOM 2008). Since 1976, six stations have been fished at Vendelsö between 9 and 12 consecutive nights both in April and August every year, generating an effort of 108 to 144 fyke net nights per year. At each of the six stations, two fyke nets have been placed perpendicular to the shore, covering a transect from 2 to 5 m depth. At each sampling occasion, the abundance of all fish and larger crustaceans have been registered, as well as water temperature, Secchi depth and salinity (for more info, see Thoresson 1996). The August sampling better represents changes in wrasse and shore crab populations (20 and 5 times higher catch in August compared to April, respectively). However, gobiids are as common in April as in August, and we therefore included both sampling periods in our analyses of coastal mesopredators. Data were square-root or $\log_{10}$-transformed if necessary to improve linearity and temporal trends were analysed with linear regression. We tested all analysed time series for autocorrelation to the 15$^{th}$ lag using the autocorrelation function (STATISTICA, version 8.0, StatSoft, Inc. 2007). All coastal and later analysed offshore time series, showed significant first-order autocorrelations (dependence on the first lag), which may cause an underestimation of the standard error and a higher risk of Type 1 error. We therefore adjusted sample sizes for first-order autocorrelation by calculating effective sample sizes: effective sample size ($N^*$) = sample size (N) × $(1 - r_c)/(1 + r_c)$, where $r_c$ is the first-order autocorrelation coefficient (Dawdy and Matalas 1964). In the results, $F^*$ and $P^*$ indicate that sample sizes are corrected for significant first-order autocorrelations. Since 1976, the abundance of the dominating wrasses, corkwing wrasse *Symphodus melops* (L) and Goldsinny wrasse *Ctenolabrus rupestris* (L), has steadily increased in the catches (linear regression: N = 34, R = 0.49, $F^*_{1;11} = 10.26$, $P^* = 0.009$), as has the common shore crab (linear regression: N = 34, R = 0.49, $F^*_{1;12} = 22.29$, $P^* < 0.001$) and black goby, *Gobius niger* (linear regression on square-root trans-formed data: N = 34, R = 0.72, $F^*_{1;8} = 34.80$, $P^* <$

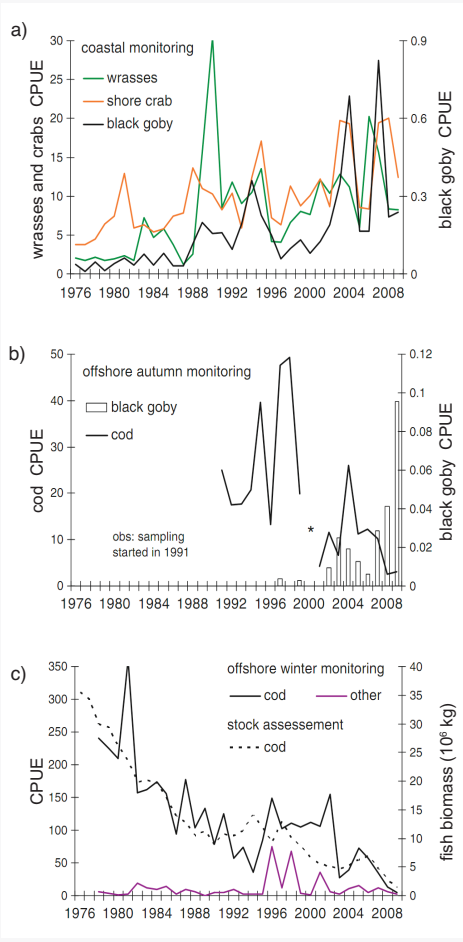


**Figure 6.1** Trends in larger predatory fish and mesopredators in Kattegat, ICES subdivision 21, the North Sea. **a)** Abundances of mesopredators in the coastal monitoring at Vendelsö by the Swedish Board of Fisheries: *Gobius niger* (black goby - black line), *Symphodus melops* and *Ctenolabrus rupestris* (corkwing wrasse and Goldsinny wrasse - green line) and *Carcinus maenas* (shore crab - orange line). CPUE denote catch (numbers) per night per fyke net. Note that *Symphodus melops* was five times more common than *Ctenolabrus rupestris* and therefore dominated the trend for wrasses. **b)** Autumn abundances of black goby (white bars) and *Gadus morhua* (cod - black line) in offshore trawls by the International Bottom Trawl Survey (IBTS). All autumn trawls are from September. The early autumn is the main season when cod predates on black goby in nearshore habitats. Regular autumn trawls are only available within IBTS from 1991. CPUE denote catch in kg per trawl hour. Note that this survey is aimed at offshore demersal fish, and the black goby is therefore only represented by a fraction of its true abundance. In 2006, corresponding nearshore abundances of black goby averaged 92 individuals per beach seine haul in vegetated shallow bays along the Swedish Atlantic coast (Pihl et al. 2006). Asterisk indicates that there is no data from the autumn of 2000. **c)** Winter abundances of cod (black line) and other larger demersal predators (*Melanogrammus aeglefinus* (L) (haddock), *Molva molva* (L) (ling); and *Pollachius pollachius* (L) (pollack)) in offshore trawls (IBTS), and stock assessment of the total biomass of cod in the Kattegat over time. Scientfic winter trawls for demersal fish have been performed in February since 1978. CPUE denote catch in kg per trawl hour.



0.001; Figure 6.1a). During the same time (1976–2009), the powerplant at Ringhals has also increased its effect and there is a significant increase in water temperatures in the area affected by cooling water (Bergström et al. 2009, www.fiskeriverket.se). At Vendelsö, there is a marginally significant trend towards increasing water temperatures in August ($R = 0.33$, $F_{1;32} = 3.84$, $P = 0.059$), but not in April ($R = 0.28$, $F_{1;32} = 2.80$, $P = 0.103$). However, the temperature increase at Vendelsö in August corresponds to ca. a 0.5 °C per decade, which is comparable to the general increase in surface water temperatures in the whole Kattegat area and significantly lower than the temperature increase measured at the nuclear power plant (Swedish Board of Fisheries 2008, Bergström et al. 2009, www.fiskeriverket.se). In all, this suggests that the increase in effect at the powerplant at Ringhals has not had a major impact on the temperature increase at Vendelsö. Note that the densities of black goby are relatively low in this program, since the catchability of the

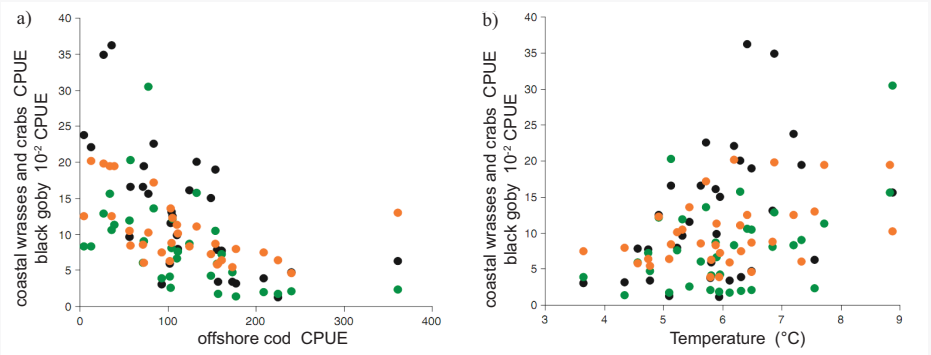


**Figure 6.2** Relation between coastal abundances of the mesopredators black goby (black dots), wrasses (group of small-bodied fish - green dots), and shore crabs (orange dots) on the Kattegat coast of Sweden, and **a)** offshore abundances of cod in winter (February), and **b)** coastal temperatures in spring (April). Offshore cod was sampled by the International Bottom Trawl Survey (IBTS). CPUE for cod denote catch per trawl hour. Coastal abundances of mesopredators and temperatures are from the coastal monitoring at Vendelsö by the Swedish Board of Fisheries (fish data includes April and August samplings). CPUE for mesopredators denote catch per night per fyke net.

species is low in fyke nets. However, increasing densities of black goby are also indicated by catches in an offshore autumn trawl survey (ICES International Bottom Trawl Survey of demersal fish in September, IBTS), where densities have increased 45 times between the 1990s and the 2000s in Kattegat (ICES subdivision 21; linear regression on square-root transformed data: N = 18, R = 0.85, $F^{*}_{1;6}$ = 43.97, $P^{*}$ = 0.001; Figure 6.1b). The increase in coastal mesopredators coincided with a long-term decreasing trend of cod populations in the international offshore bottom trawl survey in Kattegat (*Gadus morhua* L, IBTS average catch weight kg per trawl hour in September: linear regression on square-root transformed data, N = 18, R = -0.65, $F^{*}_{1;10}$ = 11.70, $P^{*}$ = 0.001, Figure 6.1b; IBTS in February: linear regression, N = 18, R = -0.77, $F^{*}_{1;7}$ = 43.26, $P^{*}$ < 0.001, Figure 6.1c). Cod is the dominant larger demersal predator in the area and was subjected to a strong commercial fishery during the decline from 1970s to the 2000s. Juveniles of offshore populations of cod settle in nearshore habitats and the larger individuals predate significantly on gobiids, shore crabs and wrasses (Pihl 1982, Pihl and Ulmestrand 1993, Salvanes and Nordeide 1993). Notably, the catch of cod in the offshore bottom trawl survey was negatively correlated with the catch of mesopredators in the coastal fyke net monitoring program (Pearson's product moment correlation, wrasses [square-root transformed data] r = -0.61, N = 32, t = 4.24, P < 0.001, shore crab: r = -0.51, N = 32, t = 3.22, P = 0.003, black goby [square-root transformed data]: r = -0.64, N = 31, t = 4.58, P < 0.001; Figure 6.2a), suggesting a link between declining cod populations and the increase in mesopredators. However, general changes in climatic variability have been proposed to have generated changes in the composition of fish communities during the same time period in the North Sea, with increasing temperatures as a main driver (Alheit et al. 2005). Temperature is important for the year-class strength of many fish species. To

compare possible drivers of mesopredator abundances, we therefore constructed multiple regression models for the coastal mesopredator groups at Vendelsö, including offshore cod (catch weight kg per trawl hour in February) and average temperatures during the fyke net sampling in April and August as explanatory variables. The temperature in August did not significantly explain any variation in mesopredator abundances and was deleted from all models.

Instead, offshore biomass of cod together with water temperatures in April contributed significantly to all models (Figure 6.2, Table 6.1). The results indicate that spring temperatures are probably important for the abundance of mesopredators in the area. However, in contrast to cod biomass local spring temperatures did not change over time. Thus, the results suggest that decreasing predation pressure by juvenile cod, alongside with changed climatic variability may have contributed significantly to the increased abundances of mesopredators along the coast.

**Figure 6.3** Shallow seagrass (*Zostera marina*) bed on the Swedish Atlantic coast (Fiskebäckskil), with heavy load of filamentous macroalgae (Ectocarpales and *Ulva* spp.). Field experiments in the area show that the summer/autumn algal accumulation may partly be caused by an intense predation from highly abundant mesopredators on the most effective herbivore; adult *Gammarus locusta* amphipods (e.g. Moksnes et al. 2008). Photo: Johan Eklöf.

Black goby, shore crabs and wrasses all have the potential to regulate the abundance of crustacean and gastropod herbivores ("mesograzers"), potentially resulting in cascading effects on vegetation (Norderhaug et al. 2005, Newcombe and Taylor 2010). Concomitant with the observed changes in food web composition, beds of eelgrass (*Zostera (Zostera) marina* L) - the dominating foundation species on shallow soft-bottoms - declined with 60% on the northern Swedish Atlantic coast since the 1980s and up to 85% in northern Kattegat (Kungälv, Baden et al. 2003, Nyqvist et al. 2009). These losses have been attributed to blooms of mat-forming filamentous algae (e.g. *Cladophora* spp., Ectocarpales and *Ulva* spp.) generated by a combination of increased nutrient supply (via coastal eutrophication) and low grazing pressure, mediated by high predation pressure on functionally important grazers from high densities of mesopredators (Figure 6.3, Moksnes

**Table 6.1** Multiple regression results for coastal mesopredatory fish at Vendelsö (Kattegat), including offshore cod biomass and local temperatures in spring (April) and late summer (August) as additative explanatory variables.

| | Full model | | | Univariate results: spring biomass offshore cod | | | Univariate results: coastal spring temperatures | | |
|---|---|---|---|---|---|---|---|---|---|
| | *R* | $F_{2,29}$ | *P* | Partial correlation | $F_{1,29}$ | *P* | Partial correlation | $F_{1,29}$ | *P* |
| Wrasses (sqrt-transformed data) | 0.69 | 13.40 | **<0.001** | -0.60 | 16.61 | **<0.001** | 0.41 | 5.87 | **0.022** |
| Shore crab | 0.63 | 9.35 | **0.001** | -0.49 | 9.00 | **0.005** | 0.43 | 6.43 | **0.017** |
| Black goby (sqrt-transformed data) | 0.83 | 32.33 | **<0.001** | -0.70 | 27.14 | **<0.001** | 0.69 | 26.12 | **<0.001** |

*August temperatures never contributed significantly to the models and were therefore deleted.*

et al. 2008, Baden et al. 2010). Field experiments using cages show that predation by local mesopredators decrease the biomass of potential mesograzers by more than 95% in this system (Moksnes et al. 2008, Baden et al. 2010). Cage experiments also demonstrate that the black goby indirectly increases the biomass accumulation of ephemeral algae in seagrass patches up to five times by controlling the most efficient grazers: adult (> 9 mm) individuals of the amphipod *Gammarus locusta* (L) (Moksnes et al. 2008). Today, gammarid and isopod mesograzers occur in very low abundances in eelgrass beds, where they were abundant in the 1980s (Jephson et al. 2008, Moksnes et al. 2008, Baden et al. 2010). Thus, the decrease in offshore populations of mesopredators described here for Kattegat, might have impacted crucial components of these nearshore ecosystems, including their nursery function for the top predators already impacted by fishing. However, even though these results indicate that altered cross ecosystem interactions have fundamentally impacted the coastal ecosystem, there is still a strong need to clearly link such time-series of higher trophic levels with the experimental results from lower trophic levels in seagrass meadows.



## Increase of mesopredators on the Swedish Baltic Sea coast

There are also indications from the coast of the central Baltic Sea that offshore fisheries on cod may have cascading effects on coastal food webs. Interestingly, these cascading effects seem dependent on offshore-inshore migrations of mesopredators, combined with changes in interspecific competition, as well as release in predation pressure (Ljunggren et al. 2010). On the Swedish coast of the central Baltic Sea, juvenile three-spined stickleback (*Gasterosteus aculeatus aculeatus* L) - a smaller predatory fish feeding on crustacean and gastropod mesograzers (Eriksson et al. 2009, Sieben et al. 2011b) - completely dominate many sheltered coastal communities in early summer (Eriksson et al. 2009, Ljunggren et al. 2010). Stickleback changes distribution over the ontogeny, and after their first summer the majority migrate offshore (unpublished data). Since the 1980s, the offshore food web

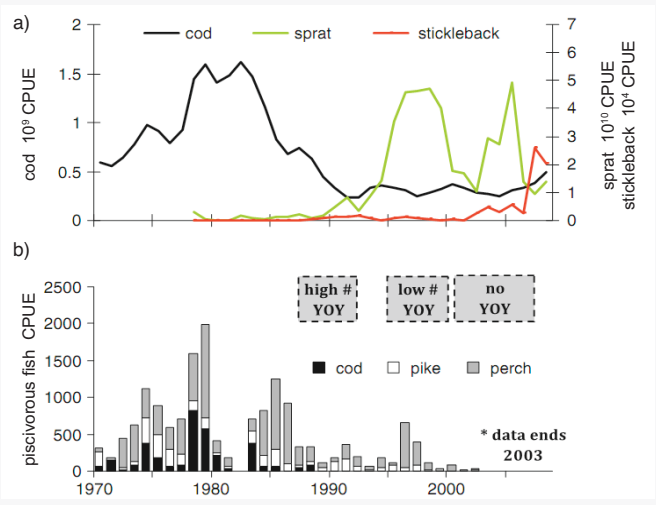


**Figure 6.4** Trends in **a)** offshore abundances of cod (stock assessment estimates, ICES 2010a), *Sprattus sprattus* (sprat, acoustic estimates from the ordinary international acoustic survey, ICES 2010b) and *Gasterosteus aculeatus* (three-spined stickleback, trawl hauls made during the ordinary international acoustic survey), and **b)** coastal abundances of larger predators: cod, *Perca fluviatilis* (European perch) and *Esox lucius* (Northern pike) together with local recruitment of perch and pike (in boxes: the number of young of the year fish YOY). **a)** Sprat and stickleback data are from ICES subdivision 27, cod data are from subdivisions 25–32. Cod and sprat are estimated total numbers, while stickleback cpue is number per trawl hour. **b)** Trap-net monitoring data (catch per night per trap) of cod, perch and pike between 1970 and 2002 from Gåsö (Mönsterås, county of Kalmar) on the southeast coast of Sweden. The Gåsö data is part of a larger time-series from four sites around a paper plant (Mönsterås bruk) which stops in 2003. Here, we present data exclusively from Gåsö, the site most affected by the open sea, because it is a good representation of fish both from the freshwater and marine communities. Full pike data is presented in Sect. 1 in the electronic supplement to Ljunggren et al. (2010). Estimates of high, low and no recruitment of perch and pike are also based on Ljunggren et al. (2010).

in the central Baltic Sea has changed dramatically, indicating a strong basin-wide mesopredator release phase (Alheit et al. 2005, Österblom et al. 2007, Casini et al. 2008, Möllmann et al. 2008). Initially, the offshore Baltic Sea cod populations declined by 75% during the 1980s, due to climate induced poor recruitment conditions combined with high fishing pressure (Figure 6.4a, ICES 2010a). This generated a trophic cascade in the open sea, including a four-fold increase in the dominating pelagic mesopredator sprat (*Sprattus sprattus* (L)), a 50% decrease in summer zooplankton biomass and a doubling in phytoplankton biomass (Casini et al. 2008). Recently, offshore abundances of stickleback have increased exponentially (Figure 6.4a, Ljunggren et al. 2010), suggesting a dramatic increase of this mesopredator also in the coastal habitat. Coastal monitoring of migrating fish is poor, but a combination of unique data from an open archipelago of the Swedish Baltic coast (the Kalmar Sound) indicates that the changes in fish community structure in the open Baltic Sea have also affected nearshore areas. In the 1970–1980s, high abundances of cod were commonly registered near the shore, but from the early 1990 cod has vanished (Figure 6.4b) concomitant with the overall collapse of the Baltic cod stock (Figure 6.4a). This suggests that the general decline in Baltic cod may have limited the distribution to offshore areas, excluding the coastal zone. From 1990, there has also been a continuous decline in the densities of the dominating larger nearshore predators – European perch (*Perca fluviatilis* L) and Northern pike (*Esox lucius* L) - in the same area

(Figure 6.4b). Thus, the recent strong increase in stickleback may have been enabled by release from predation both from coastal and offshore predators: the overwintering stickleback population may have gained from the declines in offshore cod, whereas the spawning and juvenile stickleback populations may have gained from declines of both stationary coastal predators (perch and pike) and a decreased distribution of Baltic cod. This emphasizes that changed distributions and simultaneous migrations of both larger and mesopredatory fish may be important pathways linking human impacts on offshore food webs with coastal ecosystems (see also Figure 6.6).

On the Swedish coast of the central Baltic Sea, there is evidence that the high densities of stickleback indirectly increase the load of bloom forming filamentous algae in shallow bays by controlling mesograzers (Eriksson et al. 2009, Sieben et al. 2011b). Today, fish communities in areas with low abundances of perch and pike can be dominated by abundant three-spined stickleback: an average haul with a beach seine may contain up to 3,000 individuals (standardized area 100 $m^2$, Figure 6.5). In stickleback-dominated areas, habitat quality is also impacted: almost 50% of the bays are overgrown by heavy thickets of filamentous algae (Eriksson et al. 2009, Figure 6.5). Notably, large-scale exclusions of sticklebacks (thousands of individuals removed using beach seines from 20 × 30 m enclosures) in an often overgrown bay decreased the recruitment of filamentous algae by 60% (Sieben et al. 2011a). Meanwhile, stickleback abundances are much lower in areas where perch and pike still are abundant (average haul up to 60 individuals), and only 10% of the bays are overgrown by algae. This indicates that declines in larger predators may allow for massive increases in sticklebacks and thereby cause cascading negative effects to lower trophic levels. This is confirmed by small-scale experimental exclusion of larger fish and grazers, showing that declines in larger predators - by inducing a four level

**Figure 6.5** Bloom of filamentous algae in shallow bays with high densities of three-spined stickleback on the Swedish coast of the central Baltic Sea. **Left:** From above the surface of a bay dominated by *Fucus vesiculosus* L overgrown with predominantly unbranched green microalgae (e.g. *Ulotrix* spp., *Urospora* spp.) and colonial diatoms (e.g. *Melosira* spp.). Photo: Gustav Johansson. **Right:** Under the surface in a bay dominated by *Myriophyllum* sp. and *Potamogeton* sp. overgrown with filamentous macroalgae (mainly *Cladophora glomerata* (L) Kützing, *Ectocarpus siliculosus* (Dillwyn) Lyngbye and *Pylaiella littoralis* (L) Kjellman). Photo: Ulf Bergström.

trophic cascade - increase filamentous algal growth with rates comparable to those caused by nutrient enrichment alone (Eriksson et al. 2009, Sieben et al. 2011b). Food competition and egg predation by the high abundances of stickleback may now even contribute to decreased recruitment success of perch and pike (Nilsson 2006, Ljunggren et al. 2010), and potentially "lock" the coastal food web in an alternative, mesopredator-dominated regime. Thus, overfishing of offshore cod populations may have contributed to a shift in nearshore food web structure.

## Managing interactions between nearshore communities and offshore food webs

The examples provided above makes it increasingly clear that traditional management of marine resources has severe limitations, since it often ignores interactions between the status of coastal habitats and fisheries, cross-system fluxes, predator–prey interactions as well as other ecosystem components (Pikitch et al. 2004). EBM may provide a better platform for coastal management, where one of the main objectives should be the incorporation of spatial considerations, as shown by our synthesis. Offshore and coastal resources are used at different spatial scales with the potential for cascading detrimental effects both within and across ecosystems, e.g. cascading effects from offshore exploitation of top predators on nearshore biotopes. Since cross-ecosystem management also crosses geographical and sectorial management borders and academic disciplines (e.g. coastal vs. offshore, benthic vs. pelagic, fisheries vs. water quality, or zoology vs. botany), a shift within management organization structure may be a crucial first step (Olsson et al. 2008, Österblom et al. 2010). With this we mean that measures for protecting or restoring coastal ecosystems need a broad approach addressing cumulative impacts that traditionally are managed by separate management sectors: including restoration of offshore food webs, improvements in water quality and increased habitat protection through implementation of marine protected areas (Lotze et al. 2006). Furthermore, changes in offshore and coastal food webs co-occur with major changes in large-scale hydrodynamics and transport through human engineering and climate change (Harley et al. 2006, Eriksson et al. 2010), external nutrient loading by eutrophication (Cloern 2001) and habitat destruction through coastal development and dredging (Airoldi and Beck 2007). Therefore, cascading effects of increases in mesopredator abundances will most likely interact with other human-driven changes in environmental conditions and abiotic resources, eventually altering the functions of coastal communities (Figure 6.6, Olff et al. 2009, Eriksson et al. 2010). A crucial development of EBM is to acknowledge and jointly approach these multiple and potentially interacting drivers of cross-ecosystem changes (e.g. fisheries, eutrophication and habitat destruction), instead of - as in the past - dealing with them in isolation.

For example, overexploitation of offshore fish populations has triggered governmental actions to rebuild commercially important stocks and ensure sustainable fisheries. However, single-species management of fish stocks does usually not account for the complexity of food web interactions, especially those that link different ecosystems. Our

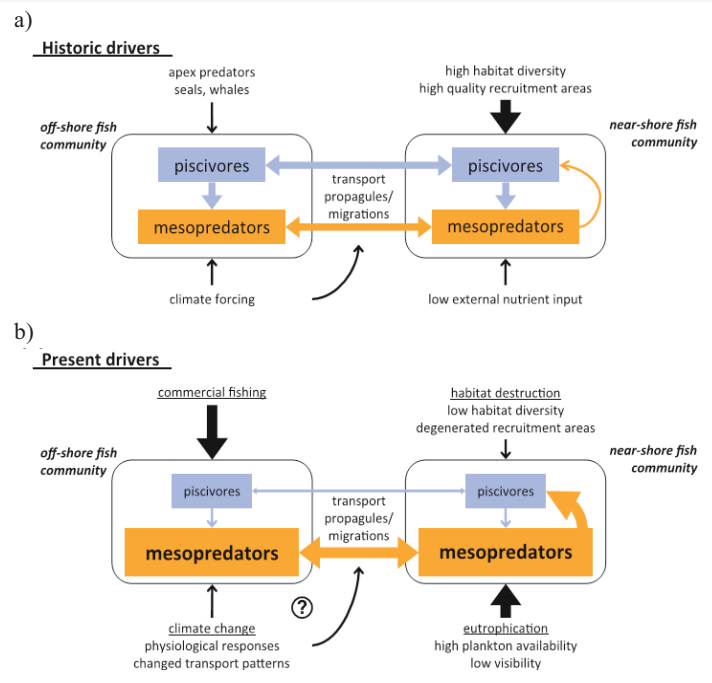


**Figure 6.6** Suggested human-driven shifts in the structure of higher trophic levels in marine food webs and resulting consequences for the relation between offshore and nearshore fish communities (see also Eriksson et al. 2010). **a)** Historic drivers: diverse communities of apex predators and natural climate forcing influenced offshore fish communities. Coastal areas had a strong function as recruitment areas for offshore fish from all trophic levels, which resulted in top-down control of the near shore fish communities. **b)** Present drivers: commercial fishing has skewed the offshore communities toward dominance by mesopredators. Such mesopredator release events increase the abundance of planktivorous and/or facultative planktivorous fish (fish that eat both plankton and benthic mesograzers) in nearshore habitats, which cause food competition and egg predation, and thereby may limit the recruitment of stationary fish. Declining populations of stationary piscivores and/or limited migrations of offshore piscivorous fish to nearshore areas in combination with increasing resource loads, may enhance bottom-up control of the nearshore ecosystem. Specific effects of climate change are not well understood (Harley et al. 2006).



results emphasize that to meet management goals for coastal areas we need to rebuild predator populations not only to maximize production of the target species, but to levels at which their ecological function is restored, both in offshore and coastal food webs. This includes increasing the abundance of offshore populations of larger predatory fish to restore their control over lower trophic levels and to restore significant migrations between offshore and coastal habitats (Figure 6.6). It also means rebuilding nearshore populations of larger predatory fish to restore their ecological function along the coast. In our case studies, this implies that to improve the quality of coastal habitats, we will need to

combine nutrient reductions and habitat restoration with fisheries specific targets. On the Atlantic coast of Sweden, we need to strengthen offshore populations of cod to promote significant coastal migrations, as well as rebuilding local nearshore populations of cod. In the Baltic Sea, we need to strengthen the cod population until its distribution area expands to include coastal habitats, and we need to rebuild local populations of pike and perch by protecting and restoring their spawning areas. These are specific case studies that span two different types of coast: one in an enclosed brackish water sea and one bordering the highly exploited North Sea continental shelf. However, offshore fisheries and coastal exploitation are global forces that have had significant effects on continental seas worldwide (Lotze et al. 2006, Worm et al. 2006). Examples from both the Pacific and the western Atlantic also support that offshore trophic cascades or changes in migration patterns of offshore predators, can have cascading effects on coastal food webs (reviewed in Baum and Worm 2009). Thus, the offshore coastal linkages described in our study systems may be relevant for a wide range of developed coasts that border highly exploited offshore systems.

## Acknowledgments

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# Synthesis

Katrin Reiss

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Fishing and eutrophication have shaped coastal ecosystems world-wide (Lotze et al. 2006). However, these two anthropogenic pressures affect marine systems in fundamentally different ways and likely interact with each other through complex food web interactions (e.g. Lotze and Milewski 2004). While fishing usually removes large predatory fish from the top-end of food webs, high nutrient loads, through run-off from land or riverine inflows, fuel primary production and thereby affect food webs from the bottom-end. Thus, to understand the human imprint on marine food webs, we need to determine how top-down and bottom-up forces and how their interactions are changed by fishing and eutrophication.

Understanding the interplay between top-down and bottom-up forces also may be an important management tool for improving the status of coastal waters. For example, the principle of trophic cascades has been used as a tool for lake management to combat eutrophication. Degraded lakes have successfully been restored through fishing out of planktivores and/or the addition of piscivores (e.g. Shapiro and Wright 1984, Carpenter et al. 1987). However, the complexity of marine food webs as well as the openness and connectivity of marine systems hamper the predictability of ecosystem changes and the application of simple manipulation tools. Accordingly, attempts of restoring open marine systems through biomanipulation have so far been absent (Lindegren et al. 2010).

The central aim of this thesis was to test joint effects of compositional changes in the fish fauna and high nutrient loads in a food web context and to investigate the interrelationship between fishing and eutrophication. A particular focus was on the functional composition of the grazer community as a key trophic link for transferring both top-down (from the fish community) and bottom-up effects (from the nutrient availability). I used an experimental approach focused on different aspects of the food web and applied on different spatial scales, from mesocosms to small-scale cage experiments to large-scale enclosures.

The key findings of my thesis are:

### A. Removal of top-predators induces a trophic cascade and increases algal biomass

In **Chapter 2**, we showed that the removal of large predators initiated a trophic cascade that eventually increased algal biomass. First, the absence of large predators increased the density of medium-sized predatory fish. Second, these meso-predators in turn caused a substantial shift in the herbivore community composition. The selective reduction of amphipods by 40-60% resulted in the dominance of gastropods. Third, this herbivore composition shift generated a 23 times higher macroalgal biomass. Most importantly, this four-level trophic cascade was only apparent under nutrient enrichment.

In **Chapter 5**, we presented results of a large-scale experiment, where higher meso-predator densities resulted in lower abundances of dominating herbivores and in a three times higher recruitment of ephemeral green macroalgae. However, herbivore composition was also dependent on the host macrophyte species and showed high variability among enclosures.

Summarising, we showed that the removal of top-predators cascaded down the food web to ultimately increase primary production both on a small and large spatial scale. However, top-down effects on producers were strongly dependent on a high nutrient availability and showed spatial variability on a large scale.

## B. Trophic effects of multiple predators depend on their identity and density

In **Chapter 3**, we showed that predator identity strongly affected the density of key herbivore groups. Species-specific impacts from fish monocultures on herbivores declined in the mixed fish assemblages due to prey-switching. However, predator identity effects on herbivores were not transmitted to the algal assemblages. Instead, algal biomass was strongly affected by predator density and nutrient enrichment and increased the algal biomass by 6- and 5-fold, respectively.

Thus, identity effects from predators in isolation were attenuated in the multiple predator assemblage, probably due to increased interference, which decreased predation pressure on the herbivores. Trophic cascading effects were dependent on predator density and nutrient enrichment, which affected algae probably through non-lethal effects on herbivores.

## C. Omnivores have the potential to buffer cascading effects

In **Chapter 4**, the presence of an omnivorous shrimp reduced the abundance of amphipods by 70–80%, while gastropod abundance remained unchanged. However, the selective predation on amphipods by the shrimp had no significant indirect effects on macroalgal biomass. In the absence of the shrimp, however, amphipods significantly reduced the biomass of ephemeral macroalgae, while gastropods strongly reduced the biomass of attached microalgae. Hence, the omnivorous shrimp has the potential to dampen cascading effects on producers by complementary feeding on both amphipods and macroalgae depending on prey availability.

Thus, we showed that omnivores have the potential to buffer cascading effects. The omnivorous shrimp controlled both the main herbivores on macroalgae (amphipods) and the macroalgae themselves by a complementary diet.



## D. The crucial role of system productivity for cascading effects

In all three included field experiments, we manipulated the nutrient availability additional to the other treatments. In **Chapter 2**, nutrient enrichment initiated cascading effects from top-predator removal on the biomass of filamentous algae. No cascading effects occurred under ambient nutrient conditions. In **Chapter 3**, nutrient enrichment enhanced cascading effects of fish density on producers. More specifically, algal biomass increased

with both increasing fish density and nutrient load and most strongly when both were combined. In **Chapter 5**, we found cascading effects of high meso-predator densities on algal recruits. Nutrient enrichment resulted in almost a doubling of algal recruits. However, algal abundances were highly variable and the effects of enrichment were statistically not significant.

Hence, nutrient enrichment enables or enhances cascading effects from predators on producers. We have indications that these cascading effects are facilitated particularly through an enhanced consumption of crustacean (gammarid) grazers at high nutrient availability.

## E. Ecosystem connectivity increases food web complexity

In **Chapter 6**, offshore and coastal monitoring data of both top-predators and meso-predators were synthesised, and a possible link between offshore fishing and coastal increases of meso-predators and ephemeral algae was discussed. On the Atlantic coast of Sweden, increases of coastal (and offshore) meso-predators correlated with offshore declines in cod stocks. At the same time, eelgrass beds declined, which was attributed to blooms of filamentous algae, partly caused by high nutrient loads and low grazing pressure. On the Baltic coasts of Sweden, cod stocks declined offshore and vanished from coastal habitats were they have been abundant earlier. Concomitantly, migrating meso-predators declined in offshore and coastal habitats. At the same time, high biomass of ephemeral algae were observed in bays with high densities of meso-predators and low densities of coastal top-predators.

Thus, it is suggested that recent increases of meso-predators are in fact triggered by offshore declines of top-predators through commercial fishing. The increasing densities of coastal meso-predators in turn cause at least locally high biomasses of ephemeral algae.

## Synthesising hypothesis

Combining these findings suggests that the strengths and interaction of top-down and bottom-up effects are mediated by the functional composition of the herbivore community. Thus, herbivores may be a key link for propagating food web effects of two anthropogenic stressors, fishing and eutrophication. It is hypothesised that the functional traits of the herbivore species determine the propagation of food web effects. Particularly, two functional groups are introduced that have opposing effects on top-down and bottom-up forces. The first group is characterised by a low resistance to predators and a high turnover rate, factors that are crucial for the initiation of a trophic cascade. The second group has, in contrast, a high predator resistance and a low turnover rate. In my study of the benthic food web, the first functional group is represented by crustaceans, which are typically soft-structured (cuticula), grow fast and reproduce quickly. Representatives of the second group include gastropods, which are usually protected by a shell, grow slowly and have a low turnover rate. Strong cascading effects are expected when the herbivore community comprises a high proportion of the first functional group. No or only weak cascading effects are expected when the second group dominates the herbivore community. Therefore, I suggest that the proportions of these two functional groups in the herbivore community determine the propagation of top-down and bottom-up effects. The following hypothetical scenarios (Figure 7.1) display food web changes, particularly the changes in the functional groups of the herbivore community that follow removal of top-predators and/or nutrient enrichment.

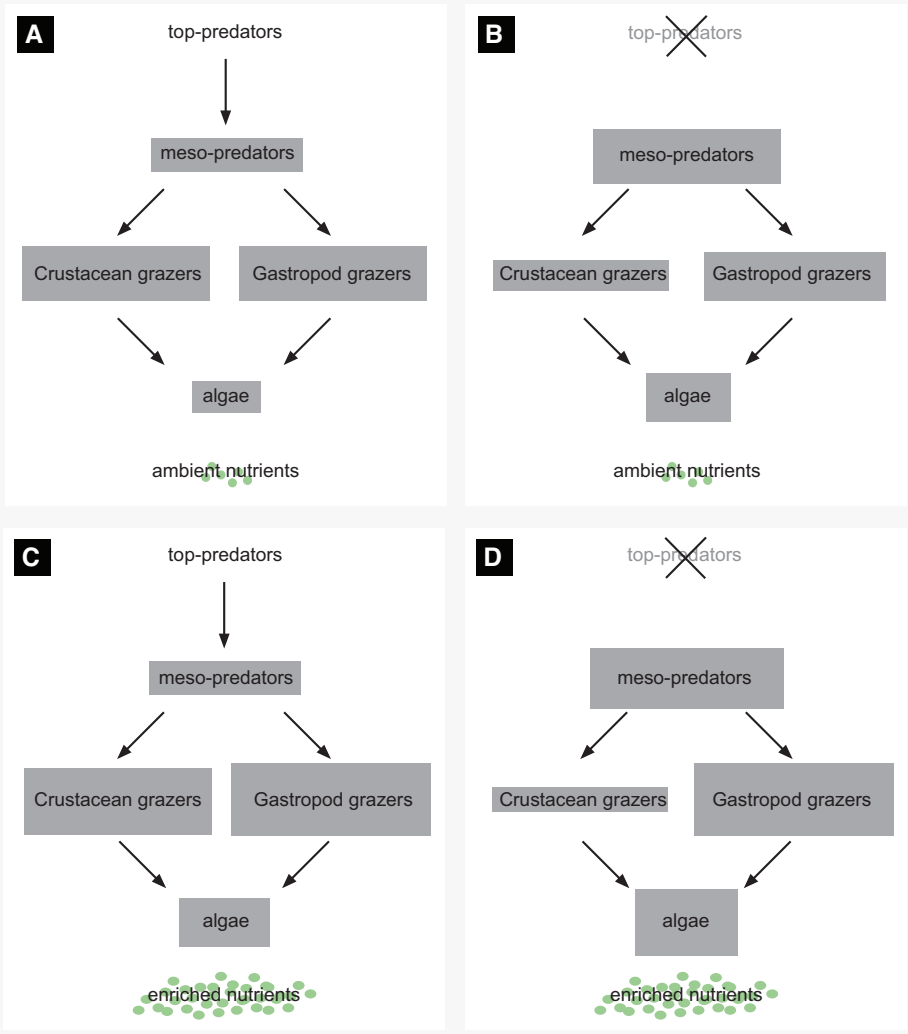


**Figure 7.1** Scenarios for interactive effects of top-predators and nutrient supply. Top-predators are present in **A**, **C** and absent in **B**, **D**. The nutrient level is low in **A**, **B** and high in **C**, **D**.
**(A)** Represents the default situation with four trophic levels in an unperturbed ecosystem.
**(B)** Low density of top-predators increases the density of meso-predators, which increases the predation pressure particularly on crustacean grazers. The less palatable gastropod grazers are not affected. Algal biomass increase from the reduced grazing pressure.
**(C)** Top-predators control the density of meso-predators. Both grazer groups benefit from the enriched nutrients through higher algal biomass, but gastropods increase stronger because of their lower predation pressure from the meso-predators.
**(D)** Low density of top-predators increases the density of meso-predators, which increases the predation pressure particularly on crustacean grazers. Crustacean grazers experience a stronger predation pressure than in (B) because of the ingestion of algae growing from enriched nutrients. Gastropod grazers benefit from enhanced algal biomass because of low predation pressure.

## Conclusions

1. A decline of top-predators through commercial fishing has, depending on system productivity, the potential to increase primary production through trophic cascading effects.

2. Predator monocultures have strong identity effects on herbivores. In multiple predator assemblages, identity effects are likely attenuated through increased interference among the predators. However, producer biomass is dependent on total predator density and nutrient enrichment.

3. Omnivores can dampen cascading effects from declining top-predators. By feeding on both herbivores and algae, omnivores may substantially influence top-down and bottom-up effects depending on competitors and prey availability.

4. A large-scale release of meso-predatory fish can increase the recruitment of benthic producers through changes in the herbivore composition. However, variability in such large-scale data is high, particularly that of the herbivore community due to a patchy distribution of their foundation macrophytes.

5. Fishery-induced food web changes can be transferred between ecosystems. Declines of offshore predators can lead to an increase of coastal meso-predators. Locally, high meso-predator densities cause higher biomass of ephemeral algae.

6. Studying ecosystem-wide effects of anthropogenic impacts is expensive in matter of time and money and results are often ambiguous due to limited control of the experimental conditions. Nevertheless, more long-term ecosystem studies are essential.

7. The functional composition of benthic herbivores (e.g. crustaceans vs. gastropods) may constitute a key link for the propagation of both top-down and bottom-up effects in coastal ecosystems. Specifically, a high proportion of herbivores with a low predator resistance in combination with high turnover rate (e.g. crustaceans) seems to be required to initiate a trophic cascade.

# Samenvatting

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Bevissing en eutrofiëring hebben wereldwijd de kustecosystemen vorm gegeven (Lotze et al. 2006). Echter, deze twee antropogenetische factoren beïnvloeden mariene systemen op een fundamenteel verschillende manier en, hoogstwaarschijnlijk, beïnvloeden elkaar via gecompliceerde interacties in het voedselweb (e.g. Lotze and Milewski 2004). Terwijl de visserij meestal de grote roofvissen uit de top van het voedselwebben verwijdert, zal een hoge nutriënten belasting, afkomstig van land of rivier, de primaire productie aanjagen en daarmee voedselwebben van onderaf beïnvloeden. Dus, om de menselijke invloed op mariene voedselwebben te begrijpen, moeten we uitzoeken hoe krachten van bovenaf (*top-down*) en onderaf (*bottom-up*) werken, en hoe hun wederzijdse beïnvloeding veranderd door bevissing en eutrofiëring.

Inzicht in het samenspel tussen *top-down* en *bottom-up* krachten kan ook dienen als een belangrijk instrument voor de verbetering van de status van kustwateren. Het principe van trofische cascades is bijvoorbeeld gebruikt als een stuk gereedschap om bij het beheer van meren de eutrofiëring te bestrijden. Zwaar verontreinigde meren werden met succes hersteld door planktoneters weg te vissen en/of viseters te introduceren (e.g. Shapiro and Wright 1984, Carpenter et al. 1987). Echter, de complexiteit van mariene voedselwebben, en ook de toegankelijkheid en connectiviteit van mariene systemen maakt het moeilijk om veranderingen in het ecosysteem te voorspellen en simpele gereedschappen toe te passen. Dat is ook de reden waarom pogingen om open mariene ecosystemen door biomanipulatie te restaureren tot nu toe uit zijn gebleven (Lindegren et al. 2010).

Het centrale doel van dit promotieonderzoek was het testen de gezamenlijke effecten van veranderingen in de samenstelling van vis fauna en hoge nutriënt belastingen in een voedselweb context en om de onderlinge beïnvloeding van bevissing en eutrofiëring te onderzoeken. Speciale aandacht werd gegeven aan de functionele samenstelling van de grazersgemeenschap die een trofische sleutelpositie inneemt bij de overdracht van zowel *top-down* (vanuit de vis gemeenschap) en *bottom-up* (vanuit de nutriënten beschikbaarheid) effecten. Ik gebruikte een experimentele benadering gericht op verschillende aspecten van het voedselweb toegepast op verschillende schalen, van *mesocosms* tot kleinschalige kooi experimenten tot grootschalige omsluitingen.

De voornaamste resultaten van mijn onderzoek zijn:

### A. Verwijderen van top-predatoren induceert een trofische cascade en verhoogt de algen biomassa

In **Hoofdstuk 2** tonen wij aan dat het verwijderen van grote predatoren een trofische cascade initieerde, die uiteindelijk de algen biomassa deed toenemen. In eerste instantie nam, door de afwezigheid van grote predatoren, de dichtheid van middelgrote roofvissen toe. Daarop veroorzaakten deze *meso*-predatoren een aanzienlijke verschuiving in de samenstelling van de herbivore gemeenschap. Tot slot genereerde deze herbivore

gemeenschap een 23-voudig hogere macroalgen biomassa. Belangrijk is dat deze viertraps trofische cascade alleen optrad bij verrijking met nutriënten.

In **Hoofdstuk 5** presenteren wij de resultaten van een grootschalig experiment waarbij hogere *meso*-predatoren dichtheden resulteerde in lagere hoeveelheden dominante herbivoren en een driemaal hogere rekrutering van efemere groene macroalgen. Echter, de samenstelling aan herbivoren was ook afhankelijk van macrofyte gastsoort en vertoonde grote variabiliteit tussen de omsluitingen.

Samenvattend: Wij toonden aan dat het verwijderen van top-predatoren door het voedselweb naar beneden toe doordrong om uiteindelijk de primaire productie toe te laten nemen op zowel een kleine als grote ruimtelijke schaal. Echter, *top-down* effecten op deze producenten was sterk afhankelijk van een hoge beschikbaarheid van nutriënten en vertoonde ruimtelijk variabiliteit op de grote ruimtelijke schaal.

### B. Trofische effecten van verschillende predatoren is afhankelijk van hun identiteit en dichtheid

In **Hoofdstuk 3** tonen wij aan dat de identiteit van de predator de dichtheid van belangrijke herbivore groepen sterk beïnvloedde. Soort specifieke effecten van vissen in monocultuur namen af in gemengde vis gemeenschappen als gevolg van prooi-wisselen. Echter, deze effecten van de predator identiteit werden niet doorgegeven aan de algen gemeenschappen. In plaats daarvan werd de algen biomassa sterk beïnvloed door zowel de predator dichtheid en als de nutriënten verrijking. De algen biomassa nam hierdoor toe met een factor van respectievelijk 6 en 5.

Dus, individuele effecten van geïsoleerde predatoren verdwenen in de meervoudige predator gemeenschap, waarschijnlijk door een toegenomen onderlinge interactie waardoor de predatiedruk op de herbivoren afnam. Trofische cascade effecten waren afhankelijk van de predatoren dichtheid en nutriënten verrijking, welke de algen beïnvloedde, waarschijnlijk via niet-lethale effecten op de herbivoren.

### C. Omnivoren hebben het potentieel om cascade effecten te bufferen

In **Hoofdstuk 4** wordt beschreven dat de aanwezigheid van een omnivore garnaal de dichtheid van amphipoden 70-80% reduceert, terwijl de dichtheid van gastropoden onveranderd blijft. Echter, de selectieve predatie van amphipoden door garnalen had geen significante indirecte effecten op de biomassa van de macroalgen. Echter, bij afwezigheid van de garnaal reduceerden de amphipoden de biomassa van efemere macroalgen significant, terwijl de gastropoden de biomassa van aangehechte microalgen sterk reduceerden. Dat betekent dat de omnivore garnaal het potentieel heeft om cascade effecten op producenten te dempen door aanvullend te foerageren op zowel amphipoden als macroalgen afhankelijk van de beschikbaarheid van prooi.

Hiermee demonstreerden wij dat omnivoren het potentieel hebben om cascade effecten te bufferen. De omnivore garnaal controleerde door een aanvullend dieet zowel de belangrijkste macroalgen etende herbivoren (amphipoden) als de macroalgen zelf.

### D. De cruciale rol van de productiviteit van het systeem voor cascade effecten

In alle drie betrokken veldexperimenten, manipuleerden wij de beschikbaarheid aan nutriënten als aanvulling op de andere behandelingen. In **Hoofdstuk 2** initieerde de nutriënten verrijking cascade effecten op de biomassa van filamenteuse algen als de top-predatoren waren verwijderd. Deze cascade effecten vonden niet plaats bij normale nutriënt niveaus. In **Hoofdstuk 3** bevorderde de nutriënten verrijking cascade effecten via de dichtheid van vissen op de producenten. Meer in detail: De algen biomassa nam toe zowel bij een toenemende dichtheid aan vissen als een hogere nutriënten belasting, en was het sterkste als beide factoren gecombineerd werden. In **Hoofdstuk 5** vonden we cascade effecten van hoge *meso*-predatoren dichtheden op algen rekruten. Nutriënt verrijking veroorzaakte bijna een verdubbeling aan algen rekruten. Echter, de algen dichtheden waren erg variabel en het effect van de verrijking was niet significant.

Dus nutriënten verrijking bevorderd/versterkt cascade effecten van predatoren op producenten. Wij hebben aanwijzingen dat deze cascade effecten in het bijzonder gefaciliteerd worden door een toegenomen consumptie van kreeftachtige (gammariden) grazers bij een hogere beschikbaarheid van nutriënten.

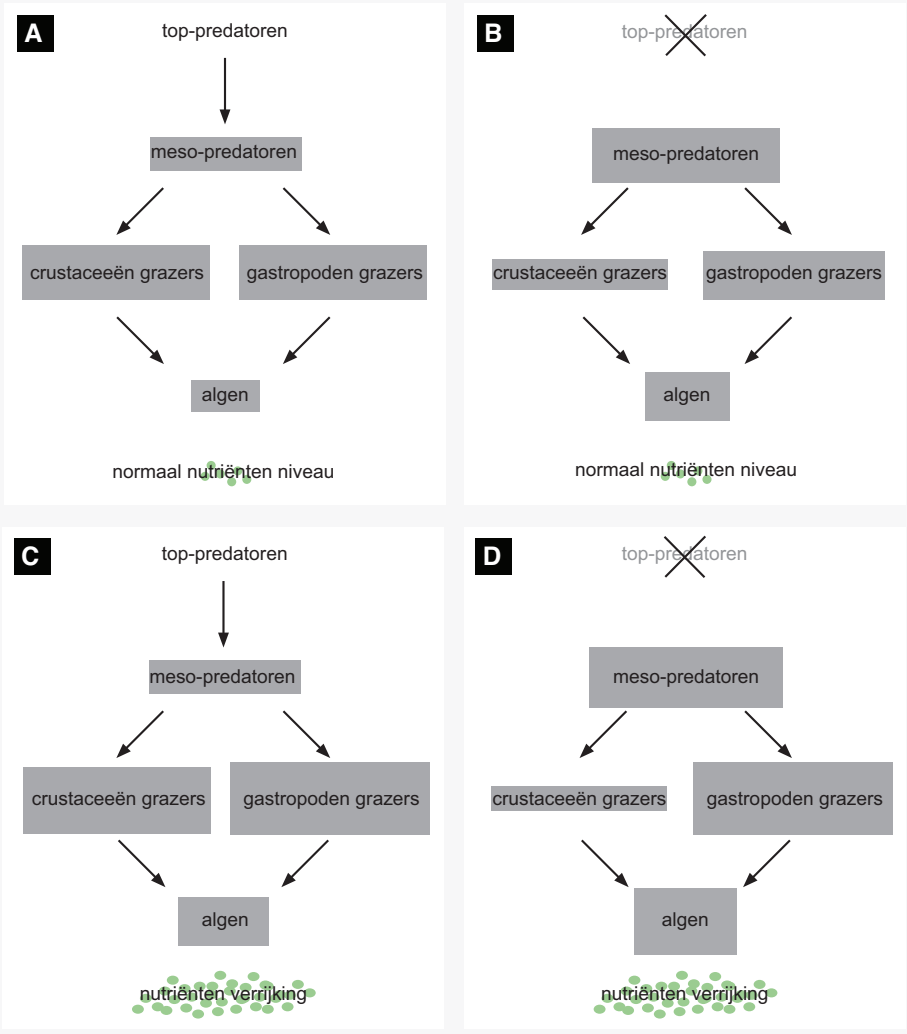
### E. Ecosysteem connectiviteit bevorderd voedselweb complexiteit

**Hoofdstuk 6** beschrijft de synthese van gegevens van waarnemingen van top- en *meso*-predatoren in open zee en langs de kust, en bediscussieert het mogelijke verband tussen visserij op de open zee en de toename van *meso*-predatoren en efemere algen. Langs de Atlantische kust van Zweden is de toename van kustgebonden (en volle zee) *meso*-predatoren gecorreleerd met een afname van de kabeljauwstand in open zee. Tegelijkertijd gingen de zeegrasbedden achteruit wat werd verweten aan bloeien van filamenteuse algen gedeeltelijk veroorzaakt door hoge nutriënt belasting en lage graasdruk. Langs de Baltische kust van Zweden nam de kabeljauwstand in open zee af en verdween volledig uit de kustgebonden habitats, waar ze voorheen rijk vertegenwoordigd waren. Parallel hiermee was er een afname van migrerende *meso*-predatoren langs de kust en in open zee. Tezelfdertijd werd een hoge biomassa van efemere algen waargenomen in baaien met hoge dichtheden aan *meso*-predatoren en lage dichtheden aan top-predatoren.

Samenvattend wordt hiermee de suggestie gewekt dat de toename aan *meso*-predatoren in feite aangewakkerd wordt de afname van top-predatoren door de commerciële visserij. Op hun beurt veroorzaken de toenemende dichtheden van kustgebonden *meso*-predatoren op lokaal niveau een hoge biomassa aan efemere algen.

### Samenvattende hypothese

Samengevoegd suggereren deze resultaten dat de krachten van en interacties tussen *top-down* en *bottom-up* effecten gestuurd worden door de functionele samenstelling van de herbivore gemeenschap. Daarom spelen herbivoren een sleutelrol bij de verspreiding van effecten op het voedselweb door twee antropogene stressfactoren, visserij en eutrofiëring. Dit leidt tot de hypothese dat de functionele eigenschappen van de herbivore soorten de verspreiding van effecten op het voedselweb bepalen. In het bijzonder die twee functionele groepen die tegengestelde effecten op de *top-down* en *bottom-up* krachten hebben. De eerste groep wordt gekarakteriseerd door een lage weerstand tegen predatoren en een snelle opeenvolging van generaties (*turnover rate*) - factoren die cruciaal zijn voor het op gang brengen van een trofische cascade. De tweede groep heeft echter een hoge weerstand tegen predatoren en een trage opeenvolging van generaties. In mijn onderzoek aan het benthische voedselweb wordt de eerste groep vertegenwoordigd door crustaceeën, getypeerd door hun zachte structuur (cuticula), en snelle groei en reproductie. Vertegenwoordigers van de tweede groep bestaat uit gastropoden met meestal de bescherming van een schelp, langzame groei en trage opeenvolging van generaties. Wanneer de tweede groep de herbivore gemeenschap domineert kunnen geen (of zeer zwakke) cascade effecten kunnen verwacht worden. Dit alles leidt tot de vaststelling dat de onderlinge verhoudingen van deze twee functionele groepen in de herbivore gemeenschap de verspreiding van *top-down* en *bottom-up* effecten bepalen. De volgende hypothetische scenario's (Figuur 7.2) laten voedselweb veranderingen zien, in het bijzonder de veranderingen in de functionele groepen van de herbivore gemeenschap die volgen op de verwijdering van top-predatoren en/of nutriënt verrijking.




**Figuur 7.2** Scenario's voor interactieve effecten van top-predatoren en nutriënten aanvoer. Top-predatoren zijn aanwezig in **A**, **C** en afwezig in **B**, **D**. Het nutriënten niveau is laag in **A**, **B** en hoog in **C**, **D**.
**(A)** Laat de standaard situatie zien met de vier trofische niveaus in een ongestoord ecosysteem.
**(B)** Lage dichtheden van top-predatoren verhoogt de dichtheid van meso-predatoren, waardoor de begrazingsdruk op speciaal de crustaceeën grazers toeneemt. De minder smakelijke gastropoden grazers worden niet beroerd. De algen biomassa neemt toe als gevolg van de verminderde begrazingsdruk.
**(C)** Top-predatoren controleren de dichtheid van meso-predatoren. Beide groepen grazers profiteren van de nutriënten verrijking middels een hogere algen biomassa, maar de gastropoden nemen sneller toe vanwege de lagere predatiedruk door de meso-predatoren.
**(D)** Door een lage dichtheid aan top-predatoren neemt de dichtheid aan meso-predatoren toe, waardoor de predatiedruk op speciaal crustaceeën grazers toeneemt. Die grazers ondervinden een sterkere predatiedruk dan in (B) als gevolg van consumeren van de algen die op de verrijkte nutriënten groeien. Gastropoden grazers halen voordeel uit de toegenomen algen biomassa vanwege een lage predatiedruk.

## Conclusies

1. Een afname van top-predatoren door commerciële visserij heeft het potentieel om primaire productie toe te laten nemen via trofische cascade effecten, dit afhankelijk van de productiviteit van het systeem.

2. Monocultures van predatoren hebben sterke individuele effecten op herbivoren. In meervoudige predator gemeenschappen worden de individuele effecten waarschijnlijk afgezwakt door een toegenomen interactie tussen de predatoren. Echter, de biomassa van de producenten is afhankelijk van de totale predator dichtheid en de nutriënten verrijking.

3. Omnivoren kunnen de cascade effecten van afnemende aantallen top-predatoren dempen. Door zowel op herbivoren als op algen te foerageren, kunnen omnivoren de *top-down* en *bottom-up* effecten significant beïnvloeden, dit afhankelijk van de beschikbaarheid van concurrenten en prooi.

4. Een grootschalige uitbraak van *meso*-predatore vissen kan het rekruteren van benthische producenten verhogen via veranderingen in de samenstelling van herbivoren. Echter, de variabiliteit in deze grootschalige gegevens is hoog, in het bijzonder die van de herbivore gemeenschap als gevolg van een onregelmatige verspreiding van de macrofyte gastsoorten.

5. Voedselweb veranderingen geïnduceerd door visserij kunnen tussen ecosystemen uitgewisseld worden. Vermindering van open zee predatoren kan leiden tot een toename van kustgebonden *meso*-predatoren. Op lokale schaal veroorzaken hoge *meso*-predator dichtheden een hogere biomassa aan efemere algen.

6. Bestuderen van ecosysteem brede effecten van antropogene invloeden is duur, zowel in tijd als in geld. De resultaten zijn vaak onzeker als gevolg van de beperkte controle over de experimentele omstandigheden. Toch zijn meer lange termijn ecosysteem studies noodzakelijk.

7. De functionele samenstelling van benthische herbivoren (d.w.z. crustaceeën versus gastropoden) kunnen een sleutelrol spelen bij de verspreiding van *top-down* en *bottom-up* effecten in kustecosystemen. Meer in detail: Een hoger aandeel aan herbivoren met een lagere weerstand tegen predatoren in combinatie met een snelle opeenvolging van generaties (d.w.z. crustaceeën) lijkt de voorwaarde te zijn voor de aanzet tot een trofische cascade.

# Zusammenfassung

7

7

Menschen nutzen Ökosysteme heutzutage in vielfältiger Weise. Diese anthropogene Nutzung wirkt auf unsere Meere hauptsächlich durch zwei Stressfaktoren: Fischerei und Eutrophierung (durch übermäßigen Nährstoffeintrag). Die Auswirkungen beider Stressfaktoren auf marine Ökosysteme sind dabei sehr verschieden. Kommerzielle Fischerei ist zumeist auf große Raubfische (Top-Prädatoren) ausgerichtet, und entnimmt dem Ökosystem daher Biomasse hauptsächlich vom oberen Ende der Nahrungskette. Im Gegensatz dazu erhöht der Eintrag von Nährstoffen, die entweder ausgewaschen werden und dann von Land abfließen oder durch Flüsse in die Meere gelangen, die Primärproduktion und wirkt somit auf das untere Ende der Nahrungskette. Darüber hinaus können sich beide Stressfaktoren in ihrer Wirkung auch gegenseitig beeinflussen: sich verstärken, sich abschwächen oder auf andere Weise ihre Effekte modulieren. Konkret bedeutet dies, dass die Entnahme von Fischen durch Fischerei die Auswirkungen überschüssiger Nährstoffe auf das Ökosystem, und damit die Eutrophierung, verändern kann. Umgekehrt kann der Grad der Eutrophierung die Auswirkungen der Fischerei auf ein Ökosystem beeinflussen. Diese wechselseitige Beeinflussung funktioniert dabei über komplexe Veränderungen in Nahrungsnetzen, deren langfristige Konsequenzen schwer vorhersagbar sind.

Das Prinzip der trophischen Kaskade (indirekte reziproke Effekte in der Nahrungskette) wird schon seit den 80er Jahren im Gewässermanagement eingesetzt, um Eutrophierungseffekten entgegen zu wirken. Eutrophierte Seen konnten durch Biomanipulation, z.B. das Abfischen von planktivoren Fischen oder das Zusetzen von Raubfischen, renaturiert werden (z.B. Shapiro & Wright 1984, Carpenter et al. 1987). Großräumige Versuche die Biomanipulation auch in offenen marinen Gewässern (z.B. in der Küstenzone) anzuwenden fanden jedoch bisher kaum statt (Lindegren et al. 2010). Die Simulation einer großräumigen Biomanipulation konnte allerdings zeigen, dass die Entnahme von Sprotten (kleine planktivore Fische, die Kabeljaueier fressen und Nahrungskonkurrenten junger Kabeljaue sind) den geringen Bestand von Kabeljau nicht verbessert hat (Lindegren et al. 2010). Die Methoden des Binnengewässer-Managements lassen sich folglich nicht ohne weiteres auf marine Systeme anwenden. Die Gründe dafür liegen in der Verschiedenheit limnischer und mariner Systeme. Zum Einen sind marine Ökosysteme, im Gegensatz zu limnischen Systemen, offen und somit mehrfach mit anderen Systemen verbunden (z.B. die Küstenzone mit dem Land sowie mit dem offenen Meer). Zum Anderen ist die Komplexität mariner Nahrungsnetze ungleich höher als die limnischer Nahrungsnetze. Diese „Offenheit" mariner Systeme und die Komplexität ihrer Nahrungsnetze erschweren die Vorhersagbarkeit von Veränderungen in marinen Ökosystemen (z.B. durch Fischerei oder Nährstoffeintrag) zusätzlich.

Ein zentraler Aspekt dieser Dissertation war es, die Wechselbeziehung zweier anthropogener Faktoren auf ein marines Ökosystem zu untersuchen: die Entnahme von Raubfischen und eines hohen Nährstoffeintrags. Dazu wurden Experimente im Feld sowie in Mesocosmen an Land durchgeführt. Ein besonderer Schwerpunkt lag auf der

funktionellen Zusammensetzung der Herbivoren-Gemeinschaft, die eine Schlüsselrolle spielt in der Weiterleitung trophischer Effekte vom oberen sowie vom unteren Ende der Nahrungskette.

Die wichtigsten Erkenntnisse meiner Dissertation sind:

### A. Die Entnahme von Top-Prädatoren induziert eine trophische Kaskade und erhöht darüber die Primärproduktion

In **Kapitel 2** haben wir gezeigt, dass sich die Dichte kleinerer Raubfische (Meso-Prädatoren) in Abwesenheit von Top-Prädatoren erhöhte. Diese Zunahme an Meso-Prädatoren verringerte allerdings nicht die Gesamtzahl an Herbivoren (ihrer Beute), veränderte aber deutlich deren Artenzusammensetzung: Amphipoden wurden mit 40-60% besonders stark reduziert, was dazu führte, dass Gastropoden die Herbivoren-Gemeinschaften dominierten. Diese Artenverschiebung in der Herbivoren-Gemeinschaft erhöhte wiederum die Biomasse von Makroalgen um das 23fache. Diese trophische Kaskade über vier Stufen trat jedoch nur auf, wenn die Umgebung mit Nährstoffen angereicherter war.

In **Kapitel 5** haben wir in einer großräumigen Studie gezeigt, dass eine hohe Dichte an Meso-Prädatoren die Anzahl der dominierenden Herbivoren derart verringerte, dass sich 3mal mehr Algen ansiedeln konnten. In dieser Studie wurde die Verteilung der Herbivoren aber auch stark von der Makrophytenart, mit der die Herbivoren assoziiert waren, beeinflusst sowie von kleinräumigen Unterschieden im Untersuchungsgebiet.

Zusammenfassend konnten wir zeigen, dass die Entnahme von Top-Prädatoren Effekte auf das Nahrungsnetz hatten, die sich bis zu den Primärproduzenten fortpflanzten und deren Biomasse erhöhten. Das konnte kleinräumig sowie großräumig gezeigt werden. Die Effekte der Top-Prädatoren auf die Produzenten waren dabei abhängig vom Nährstoffangebot der Umgebung (Kapitel 2) und räumlich variabel (Kapitel 5).

### B. Trophische Effekte mehrerer Prädatoren sind abhängig von deren Identität und Dichte



In **Kapitel 3** haben wir gezeigt, dass die Räuberidentität die Auswirkungen der Räuber auf die wichtigsten Herbivorenarten bestimmt. In Monokulturen hatten die Räuber stark artspezifische Effekte auf die Herbivoren. Sobald die Räuber aber zusammen in einer Gemeinschaft waren, wurden diese artspezifischen Effekte abgeschwächt, wahrscheinlich ausgelöst durch einen Wechsel im Beutespektrum der Räuber. Die räuberspezifischen Effekte auf die Herbivoren hatten jedoch keinen Einfluss auf die Algengemeinschaft. Vielmehr bestimmten sowohl die Gesamtzahl der Räuber sowie das Nährstoffangebot das Algenwachstum und erhöhten die Algenbiomasse um das 6- bzw. das 5-fache.

Folglich wurden artspezifische Effekte, die die Räuber in Monokultur zeigten, in einer Räuber-Gemeinschaft abgeschwächt. Eine erhöhte Konkurrenz innerhalb der Räuber-Gemeinschaft hat wahrscheinlich das Beutespektrum der Räuber verschoben und somit den Prädationsdruck auf die Herbivoren verringert. Die Ausbildung einer trophischen Kaskade war wiederum abhängig vom Nährstoffangebot der Umgebung und der Räuberdichte, die vermutlich indirekte Effekte auf die Herbivoren hatte.

### C. Omnivore können trophische Kaskaden abschwächen

In **Kapitel 4** wurde beschrieben, dass eine omnivore Garnele die Anzahl an Amphipoden um 70 bis 80% reduzierte, während die Anzahl an Gastropoden unverändert blieb. Diese selektive Prädation auf Amphipoden hatte jedoch keinen Einfluss auf die Biomasse der Makroalgen, obwohl die Amphipoden in Abwesenheit der Garnele die Makroalgenbiomasse deutlich verringern. Gastropoden hingegen reduzierten die Biomasse von Mikroalgen. Demzufolge konnte die omnivore Garnele die trophische Kaskade abschwächen indem sie, je nach Verfügbarkeit, Amphipoden und/oder Makroalgen fraß.

Wir konnten somit zeigen, dass Omnivore das Potential haben, die Effekte trophischer Kaskaden abzuschwächen. Die omnivore Garnele wies eine komplementäre Ernährung auf und konsumierte sowohl den wichtigsten Konsumenten der Makroalgen (Amphipoden) als auch die Makroalgen selbst.

### D. Die Produktivität des Systems spielt eine entscheidende Rolle für die Ausbildung trophischer Kaskaden

In allen hier vorgestellten Feldexperimenten wurde zusätzlich zu den jeweils Experiment-spezifischen Manipulationen das Nährstoffangebot verändert. In **Kapitel 2** wurde gezeigt, dass die Entnahme von Top-Prädatoren nur eine trophische Kaskade auslöste, wenn das Nährstoffangebot hoch war. In **Kapitel 3** zeigten wir, dass eine hohe Nährstoffkonzentration die kaskadenförmigen Effekte der Fischdichte auf die Algenbiomasse verstärkt. Genauer gesagt haben sowohl eine hohe Fischdichte als auch ein hohes Nährstoffangebot zu einem erhöhten Algenwachstum geführt, besonders stark aber haben beide Faktoren zusammen gewirkt. Im selben Experiment hat ein hohes Nährstoffangebot außerdem dazu geführt, dass die Biomasse an Amphipoden abnahm, insbesondere in den Monokulturen ihres effektivsten Räubers (Barsch). In **Kapitel 5** zeigten wir, wie eine hohe Dichte an Meso-Prädatoren, über kaskadenförmige Effekte, zu einer vermehrten Ansiedlung von Algen führte. Ein hohes Nährstoffangebot verdoppelte die Zahl der Algen, wenn gleichzeitig die Zahl der Meso-Prädatoren hoch war. Allerdings waren die Algenzahlen sehr variabel und die Nährstoffeffekte nicht signifikant.

Folglich hängt sowohl die Ausbildung einer trophischen Kaskade (von Räubern auf Produzenten) als auch deren Stärke vom Nährstoffangebot der Umgebung ab. Wir fanden zudem Hinweise darauf, dass diese kaskadenförmigen Effekte besonders durch eine verstärkte Konsumierung von Amphipoden bei hohem Nährstoffangebot begünstigt werden.

### E. Die Konnektivität zwischen Ökosystemen erhöht die Komplexität in Nahrungsnetzen

In **Kapitel 6** wurden Bestandsdaten von Top-Prädatoren und Meso-Prädatoren der Küstenzone und der küstenabgewandten Zone (Offshore) miteinander kombiniert, um eine mögliche Verbindung zwischen Offshore-Fischerei und Veränderungen in der Küstenzone, und zwar einer Zunahme an Meso-Prädatoren sowie kurzlebiger Algen, aufzuzeigen. An der Westküste Schwedens korrelierten sinkende Kabeljau-Bestände in Offshore-Gebieten mit steigenden Zahlen an Meso-Prädatoren in Küsten- sowie in Offshore-Gebieten. Gleichzeitig wurde ein Rückgang an Seegraswiesen verzeichnet, der zumindest teilweise auf hohe Nährstoff-konzentrationen und abnehmende Herbivorenzahlen zurückgeführt werden konnte. An der Ostküste Schwedens gingen die Kabeljau-Bestände, ebenso wie an der Westküste, zurück, der Kabeljau verschwand jedoch auch in der Küstenzone, wo er früher häufig war. Gleichzeitig gingen die Zahlen migrierender Meso-Prädatoren in Offshore- und Küstengebieten der Ostküste zurück. In Buchten, in denen Top-Prädatoren verschwanden und Meso-Prädatoren in hoher Anzahl vorkamen, wurden auch große Mengen kurzlebiger Algen gefunden. Daher wurde vermutet, dass die kürzlichen Zunahmen von Meso-Prädatoren durch eine Abnahme von Top-Prädatoren in Offshore-Gebieten (durch Fischerei) verursacht wurden. Die zunehmende Dichte an Meso-Prädatoren in der Küstenzone verursachte wiederum zumindest lokal ein erhöhtes Wachstum kurzlebiger Algen.

### Zusammenfassende Hypothese

Zusammenfassend deuten die Ergebnisse darauf hin, dass die Ausbildung, Stärke und Wechselwirkung von Top-down- und Bottom-up-Effekten entscheidend von der funktionellen Zusammensetzung der Herbivorengemeinschaft bestimmt wird (Abbildung 7.3). Das bedeutet, dass Herbivore möglicherweise eine Schlüsselrolle einnehmen, wenn sich die Effekte zweier anthropogener Stressfaktoren (Fischerei und Eutrophierung) über das Nahrungsnetz verbreiten. Es wird die Hypothese aufgestellt, dass die funktionellen Eigenschaften der Herbivoren die Weiterleitung trophischer Effekte bestimmen. Dafür werden insbesondere zwei funktionelle Gruppen vorgestellt, die beide entgegengesetzte Rollen für der Weiterleitung trophischer Effekte im Nahrungsnetz einnehmen. Die erste Gruppe zeichnet sich durch eine geringe Widerstandsfähigkeit gegenüber Räubern sowie eine hohe Umsatzrate aus, die entscheidend für die Ausbildung einer trophischen Kaskade ist. In der vorliegenden Untersuchung des benthischen Nahrungsnetzes wird diese erste Gruppe durch Crustaceen repräsentiert, die typischerweise eine weiche Außenstruktur (Cuticula) besitzen, vergleichsweise schnell wachsen und sich reproduzieren. Die zweite Gruppe wird durch eine hohe Widerstandsfähigkeit gegen Prädatoren und eine geringe Umsatzrate charakterisiert. Vertreter der zweiten Gruppe sind hier zum Beispiel Gastropoden, die üblicherweise durch eine harte Schale geschützt sind, langsam wachsen und sich langsamer reproduzieren. Es sind also besonders die Crustaceen mit einer geringen Widerstandsfähigkeit gegen Räuber und einer hohen Umsatzrate, die entscheidend sind für die Ausbildung einer trophischen Kaskade. Falls Gastropoden die Gemeinschaft dominieren, werden hingegen nur geringe bis keine kaskadenförmigen Effekte erwartet. Ich vermute daher, dass der Anteil beider funktioneller Gruppen in der Herbivorengemeinschaft über die Weiterleitung von Top-down- und Bottom-up-Effekten entscheidet. In den folgenden hypothetischen Szenarien werden mögliche Veränderungen im Nahrungsnetz durchgespielt, die auf eine Abnahme der Top-Prädatoren und/oder Eutrophierung folgen könnten.

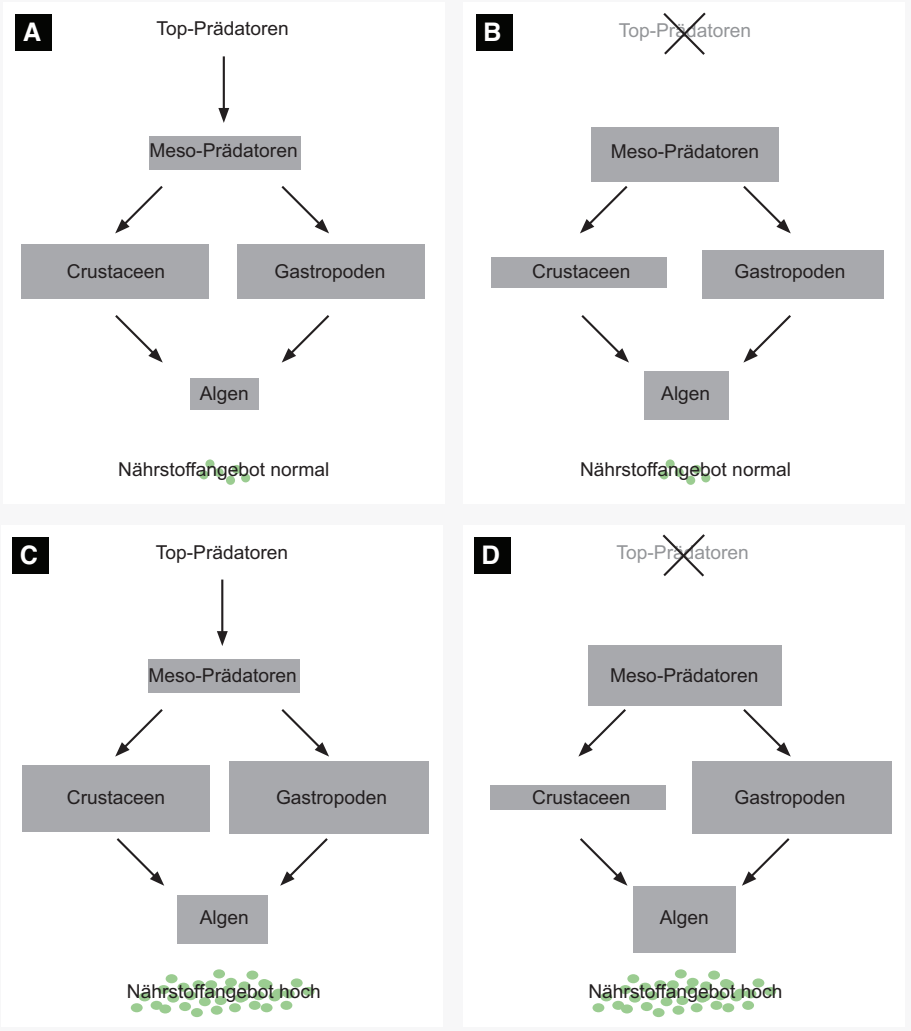



**Abbildung 7.3** Szenarien für die wechselseitigen Effekte zwischen Top-Prädatoren und Nährstoffangebot. Top-Prädatoren sind anwesend in **A**, **C** und abwesend in **B**, **D**. Das Nährstoffangebot ist gering in **A, B** und hoch in **C** ,**D**.
**(A)** Normalsituation in einem ungestörten System.
**(B)** Durch einen Rückgang an Top-Prädatoren nehmen Meso-Prädatoren zu, was den Prädationsdruck auf die Crustaceen erhöht. Die fraß-resistenteren Gastropoden werden nicht beeinflusst.
**(C)** Top-Prädatoren sind vorhanden und verhindern eine starke Zunahme an Meso-Prädatoren. Der Prädationsdruck auf die Herbivoren ist normal hoch. Ein hohes Nährstoffangebot verstärkt das Algenwachstum, wovon beide Herbivorengruppen profitieren. Gastropoden können jedoch stärker profitieren, da sie einem geringeren Prädationsdruck ausgesetzt sind.
**(D)** Durch einen Rückgang an Top-Prädatoren nehmen Meso-Prädatoren zu, was den Prädationsdruck auf die Herbivoren erhöht. Ein hohes Nährstoffangebot verstärkt das Algenwachstum, gleichzeitig aber auch den Prädationsdruck auf die Crustaceen. Gastropoden profitieren (wie Crustaceen) vom höheren Nahrunsangebot, sind zugleich aber einem geringeren Prädationsdruck ausgesetzt (im Gegensatz zu Crustaceen).

## Schlussfolgerungen

1. Ein Rückgang an Top-Prädatoren, verursacht zum Beispiel durch kommerzielle Fischerei, kann über eine trophische Kaskade zu einem Anstieg der Primärproduktion führen. Die Ausbildung und Stärke einer trophischen Kaskade hängt dabei von der Produktivität des Ökosystems ab.

2. Top-Prädatoren haben in Monokulturen starke artspezifische Effekte auf die Herbivoren. Wenn verschiedene Räuber eine Gemeinschaft bilden, werden diese artspezifischen Effekte, wahrscheinlich durch erhöhte Konkurrenz zwischen den Räubern, abgeschwächt. Die Produzentenbiomasse wird indessen am stärksten von der Gesamtzahl der Räuber sowie dem Nährstoffangebot bestimmt.

3. Omnivore Organismen können trophische Kaskaden abschwächen. Omnivore können sich zum Beispiel sowohl von Herbivoren als auch von Algen ernähren und somit, abhängig von der Nahrungsverfügbarkeit und Konkurrenten, die Weiterleitung von Top-down- und Bottom-up-Effekten maßgeblich beeinflussen.

4. Eine großräumige Zunahme an Meso-Prädatoren führte zu Veränderungen in den Herbivorengemeinschaften, die wiederum die Ansiedlung neuer Produzenten erhöhten. Jedoch war die Variabilität in den großräumigen Daten hoch. Besonders die Herbivorengemeinschaften zeigten hohe Schwankungen, verursacht durch eine geklumpte Verteilung der assoziierten Makrophyten.

5. Durch Fischerei induzierte Veränderungen im Nahrungsnetz können sich bis in andere Ökosysteme fortpflanzen. So kann ein Rückgang an Top-Prädatoren in Offshore-Gebieten die Dichte an Meso-Prädatoren der Küstenzone erhöhen. Eine hohe Dichte an Meso-Prädatoren kann wiederum, zumindest lokal, zu höheren Biomassen kurzlebiger Algen führen.

6. Die Auswirkungen anthropogener Effekte auf ein gesamtes Ökosystem zu untersuchen, ist zeitintensiv und teuer. Zudem sind die Daten oft mehrdeutig, da eine Kontrolle über die Versuchsbedingungen nur sehr begrenzt möglich ist. Es sind aber viel mehr dieser ökosystemaren Studien, besonders über längere Zeiträume, notwendig.

7. Es wird die Hypothese aufgestellt, dass die funktionelle Zusammensetzung der Herbivoren (Crustaceen und Gastropoden) eine Schlüsselrolle für die Übermittlung von Top-down- und Bottom-up-Effekten spielen könnte. Besonders ein hoher Anteil von Herbivoren mit geringer Widerstandsfähigkeit gegen Räuber und einem schnellen Lebenszyklus (z.B. Crustaceen) könnte ausschlaggebend sein für die Ausbildung einer trophischen Kaskade.

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**Pictures**

Page 10, Box 1.1: fish and shrimp pictures are from Jennings et al. 2001

Page 10, Box 1.1: alga picture is from www.fao.org

Page 11, Box 1.2: Baltic Sea oxygen concentrations from Gustafsson et al. 2012, with permission from the copyright holder (Royal Swedish Academy of Sciences)

Page 57, Box 1.5: fish pictures are from Gerstmeier and Romig 1998

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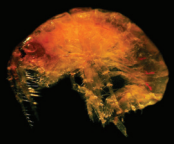
...

And, last but not least, Klemens, Serena and Karin: Thank you for the music!

# Appendix

Plate 1

## Amphipoda



*Gammarus* sp.

*Leptocheirus pilosus*

*Corophium* sp. juv.

## Bivalvia

*Cerastoderma* sp. juv.

*Macoma balthica* juv.

*Mytilus edulis*

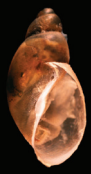
## Gastropoda

*Bithynia tentaculata*

*Peringia* (= *Hydrobia*) *ulvae*

*Ventrosia* (= *Hydrobia*) *ventrosa*

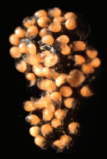
*Radix balthica*



*Radix labiata*

*Theodoxus fluviatilis*

*Tenellia adspersa*



eggs

## Isopoda

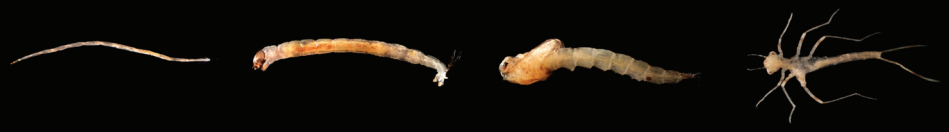
*Idotea balthica*

*Idotea chelipes*

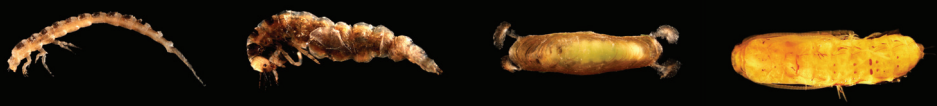
*Jaera (Jaera) albifrons*

Plate 2

## Insects



Ceratopogonidae larva | Chironomidae larva | Chironomidae pupa | Coenagrionidae larva



Haliplidae larva | Hydroptilidae larva | Hydroptilidae in case | Limnephilidae pupa

Limnephilidae case | Phryganeidae larva | Coleoptera

## Decapoda

*Palaemon adspersus*

## Mysida

*Neomysis integer*

## Polychaeta

*Nereis* sp. juv.

Plate 1 & 2: *Fucus vesiculosus*-associated fauna from the study area. Not complete. Not to scale.